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The Inheritance of Reaction to Ustilago Zeae in Maize

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CONTENTS

Page
Introduction 5
Experimental methods and materials 7
Experimental results 10
  Reactions of parent strains and crosses to smut infection 13
  Reactions of selfed lines isolated in the regular corn breeding nursery when tested in the smut inheritance plot 23
  Combination of eight low smut strains 26
  Location of smut boils on the plants of a strain 27
  A co-operative study of smut reaction conducted by the universities of Minnesota and West Virginia 29
  Seedling infection in the greenhouse 31
  Linkage studies of smut reaction 33
Discussion and conclusions 45
Summary 51
Literature cited 52

ILLUSTRATIONS

Page
Fig. 1. "Incipient," "warty," and "small" smut boils 56
Fig. 2. "Medium" and "large" smut boils, used as a basis in classifying size of smut boils 57
Fig. 3. Rustler high smut strain, culture 28 58
Fig. 4. Minnesota No. 13 strain showing smut boils on the neck of the plants as a characteristic of this strain 59
Fig. 5. Base and lower ear bud infections on a yellow endosperm liguleless strain, culture 6 60
Fig. 6. Corn seedlings growing in sand in the greenhouse bench on Jan. 8, 1927, the day they were inoculated hypodermically with smut conidia 61
Fig. 7. Smut infections on corn seedlings inoculated in the greenhouse with smut conidia, showing the location and degree of smut infection on the seedlings. Photo taken Jan. 21, 1927, the day the smut infection notes were taken 62

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THE INHERITANCE OF REACTION TO *USTILAGO ZEAE* IN MAIZE[1]

F. R. Immer[2]

Introduction

Ustilago zeae (Beckm.) Unger is one of the most destructive pathogenes affecting corn. The annual losses in the United States from this organism, in 1924, 1925, and 1926 were estimated at 1.8, 1.79, and 1.6 per cent of the total crop (57, 58, 59).[3] During years when the prevalence of corn smut approached a smut epidemic, smut destroyed the ears of from 10 to 15 per cent of some self-fertilized lines of corn grown at University Farm.

Because the organism causing corn smut can live as a parasite on corn plants or as a saprophyte in the soil for a long time, its control by cultural practices is very difficult. Infections on the plants are entirely local, making seed treatment useless. Obviously, the only method by which corn smut can be controlled is the production of resistant varieties of corn.

Corn is largely cross-pollinated (31) and the factors determining its characters are, as a consequence, largely in a heterozygous condition. In order to study the inheritance of such maize characters as resistance to disease, it is necessary first to obtain strains which are homozygous for the factors determining the characters in question. This can be accomplished by producing pure lines by selfing. Once strains have been produced which are pure for the characters in question, crosses can be made between strains differing in reaction, under given environmental conditions, and the mode of inheritance of the characters under investigation can be determined. Inbreeding decreases variability and leads to homozygosity. Many characters normally carried in the recessive condition can be isolated by inbreeding. The only result of inbreeding from an inheritance standpoint is the isolation of pure lines. Abnormal morphological, pathological, or otherwise undesirable characters are isolated in this way and may be eliminated.

The study reported in this bulletin has been a part of the general study of disease resistance conducted by the sections of plant breeding and plant pathology. The problem upon which this discussion

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[2] Grateful acknowledgment is made to Dr. H. K. Hayes, under whose direction these studies were made; to Dr. E. C. Stakman and Dr. J. J. Christensen for help with the pathological phases of the problem; and to Dr. R. J. Garber for assistance in conducting a co-operative experiment reported here.

[3] Reference by number is to "Literature Cited," p. 52.

108486

is based is a continuance of the investigation of the inheritance of reaction to *Ustilago zeae* in maize begun by Hayes, et al (32), and the determination, if possible, of the mode of inheritance of resistance or susceptibility to smut.

REVIEW OF LITERATURE

Piemeisel (56) concluded that healthy, vigorous plants from two to three feet high were most susceptible to infection by the smut-producing organism. Injury tended to increase the chances for infection but was not necessary for successful infection.

Hitchcock and Norton (33), in 1896, noticed that successively the leaves, tassels, ears, and lower nodal buds in turn became principal areas for infection because of the meristematic condition of these parts of the plant. When young leaves were infected many of the infected areas did not develop sufficiently to produce mature spores, owing, probably, to the rapid maturing of the leaf tissue and the consequent inability of the fungus to spread through the older tissue (56).

Potter and Melchers (60) concluded that infection depends not so much on the time of the season as on the stage of development of the host plant. Moisture is probably a factor in the infection of certain parts of the corn plant, but these investigators concluded that it is exceedingly doubtful, particularly in the case of ear and nodal infections, if moisture can be considered in any material degree a limiting factor in smut development under such climatic conditions as are required for the maturity of maize.

Both Pammel and Stewart (55) and Potter and Melchers (60) noted that when smut boils appear on one part of the corn plant there is a strong tendency for infections to appear also on other parts of the plant. The lower nodal buds, or rudimentary pistillate inflorescences, are some of the most common points of infection (60). Pammel and Stewart (55) concluded that if one smut boil makes its appearance on the lower nodes others often make their appearance farther up.

The location of smut boils on the plant has been found by Garber and Quisenberry (25), Hayes et al (32), and Immer and Christensen (36), to be a strain characteristic. Different strains have the majority of smut infections on different parts of the plants. This tendency is inherited from year to year.

Several investigators have studied the inheritance of smut reaction in corn. Jones (37) made crosses of several long-time selfed lines of maize and found that resistance was dominant in the F_1 and that segregation occurred in the F_2. Hayes, et al (32), from six different crosses of selfed lines, concluded that F_1 crosses of resistant strains were more resistant than either parent, while the F_1 crosses between resistant and susceptible strains produced an intermediate degree of infection. Apparently it was easy to isolate self-fertilized lines of corn which differed in their inherited reaction to smut infection in an artificially induced smut epidemic. This indicates that only a few main genetic factors were involved in determining resistance or susceptibility to smut infection.

Garber and Quisenberry (25) isolated selfed lines of corn in which the percentage of infected plants varied from 0.0 to 77.0 per cent. It was not difficult to isolate strains with an appreciable degree of resistance to smut. Resistance was constant in successive seasons' trials.

Immer and Christensen (36) presented further data on some of the selfed lines and crosses first reported by Hayes, et al (32). Their results corroborated the previous Minnesota studies in that dominance of resistance or susceptibility to smut was lacking. Further study was found to be necessary before the number of factors involved in determining certain reactions of selfed lines and crosses to corn smut could be determined.

Coffman, Tisdale, and Brandon (7), from observations of the progeny of ears from the same parent ear rows, in ear-to-row breeding tests, found differences in susceptibility to smut when corn was grown under normal field conditions. These differences were due to different female parents.

Several investigators have attempted to infect corn seedlings grown in the greenhouse, with smut. Sartoris (61) inoculated seedlings grown in sterile test tubes in the greenhouse with mycelium of *Ustilago zeae* obtained from pure cultures, but no infection resulted. He concluded that mycelium obtained in culture is unable as such to infect the host.

Arthur and Stewart (3) germinated corn between moist cloths and sprayed the seedlings with smut conidia when the plumules were about 1.5 inches long. The seedlings were then kept between moist cloths for 24 hours before being transplanted to pots. Seven of the thirteen plants inoculated developed smut.

Tisdale and Johnston (71) found corn seedlings to be as susceptible to smut infection as older plants. The same strain differences found in the field were found to exist in the greenhouse. High temperatures (80° to 95° F.) were found to favor infection. It was concluded that corn seedlings escaped infection under field conditions because of low temperature during the seedling stage. Resistant strains of corn inoculated with smut conidia were infected in the seedling stage, especially when very young, but were able to suppress invasion of the fungus to a certain extent, while susceptible plants were often killed. Resistance was internal and physiological rather than morphological. It was concluded that some internal reaction on the part of the resistant plant holds the fungus in check within the plant. Some results obtained by the use of smut from different states suggests that different physiologic forms of smut may have been used.

The work of several investigators foreshadowed the actual demonstration of the existence of physiologic forms of *Ustilago zeae*. Melchers (54), in 1921, found that cultures of smut seemed to differ in their ability to produce infections when plants were artificially inoculated. Selections and crosses of corn resistant to smut infection in one state were often more susceptible in another state. Tisdale and Johnston (71) found a difference in the ability of smut from different sources to infect corn seedlings. It remained, however, for Stakman and Christensen (68) to suggest the existence of several physiologic forms of corn smut and for Christensen and Stakman (6) actually to demonstrate the existence of at least twelve physiologic forms of *Ustilago zeae* on culture media and of seven physiologic forms differing parasitically. Some forms mutated very rapidly on culture media while others did not (6). It seems logical to conclude that a large number of physiologic forms of corn smut exist under normal field conditions.

The inheritance of quantitative characters in plants has been studied by several investigators by means of a study of their linkage relations with factors located in known linkage groups. Lindstrom (49, 52) has presented very good evidence that size factors in the tomato are linked in inheritance with the two qualitative color factors Rr and Yy.

Quantitative inheritance in the garden bean has been studied by two investigators. Sirks (65) advanced the hypothesis that size was dependent on factors controlled by an inhibiting factor, Ii, linked with a recessive color factor. Sax (62, 63, 64) presented data on linkages between seed weight and mottling and pigmentation of the seedcoat, seed weight and vine type, and yield and seedcoat characters. Sax concluded that the inheritance of yield can be determined only by a study of the linkage relations between qualitative factors whose linkage relations are known, and the factors determining yield.

Griffee (26, 27) studied the inheritance of resistance to *Helminthosporium sativum* Pammel, King and Baake in relation to certain qualitative characters in a cross of two varieties of barley. Resistance was found to be associated in inheritance with the independently inherited factor pairs for 2-rowed vs. 6-rowed, rough vs. smooth awns, and white vs. black glumes.

The inheritance of such a quantitative character as smut reaction in corn will, in all probability, be most easily determined by establishing the linkage relations between the factors determining smut reaction and known factors in the chromosome linkage groups.

EXPERIMENTAL METHODS AND MATERIALS

The selfed lines used as parents in making the crosses for this inheritance study were produced under "smut epidemic conditions" in a co-operative investigation carried on by the sections of plant breeding and plant pathology. The reactions of the parent lines from 1920 to 1924, inclusive, and of the F_1, F_2, and backcrosses between these parent lines have been previously reported (32, 36). The parent lines for these crosses were selfed lines of Minnesota No. 13, Rustler, and Longfellow. The first two varieties mentioned are dents while the last is a flint variety. The crosses were confined to selfed lines within a variety. The parental strains had relatively the same percentage of smutted plants for several years and were consequently assumed to be practically homozygous for a certain manner of reaction under conditions favorable for infection by the pathogene.

The corn was grown in rows of 28 or 42 hills each, the hills being spaced one foot apart in the row. Two seeds were planted in each hill, when sufficient seed was available, and the hills were thinned to a single plant basis when the plants were about six inches high. Except in a few cases when sufficient seed was not available, each strain or cross was replicated in two systematically distributed rows. The F_2 linkage study material, however, was grown in a separate plot in 1926, only one seed was planted per hill and the cultures were not replicated.

All plants in each culture were given a number, and notes were taken on the location and the amount of infection, if any, on each plant at three different times during the summer. The first notes were taken about August 1 for the purpose of noting the early plant infections, particularly on the leaves. About August 25 notes were again taken; this time stalk infections predominating. Notes were taken a third time about September 20, primarily to obtain data on ear infections, which were not evident on August 25. In 1926 notes were taken only twice because of abnormal weather conditions—on August 16 and September 15. In the F_2 linkage study, data were taken but once and then when it was thought that maximum infection of the plants had been reached.

The location of smut infections on the plants was noted as: S, sucker; M, main stalk; L, leaf; Se, leaf sheath; T, tassel; Mb, main stalk base; and Sh, shoot or rudimentary ear bud. Multiple infections were recorded as Mi, and incipient infections as In. The smut boils were classified into five groups according to size: In, incipient; W, warty; S, smaller than one inch in one or two diameters; M, larger than S and smaller than L; and L, larger than 4 inches in more than one diameter (see Figs. 1 and 2). In summing up the notes on total infection, the percentage of plants infected, barring incipient infection, was taken as the total percentage of infection for the strain. The smut boils classified as "incipient" dried up before ripening.

A smut epidemic was induced artificially by two methods: (1) smut spores were mixed with manure and this was spread over the plot when the seedlings were from 3 to 6 inches high. (2) Beginning when the plants were about 2 feet high and continuing until they were almost mature, the plants were sprayed with a water suspension of smut sporidia, in the evening, about every ten days. This was done under the direction of J. J. Christensen, of the section of plant pathology.

Selfed lines of corn which were apparently highly resistant to smut in the plant breeding nursery, as determined from several years' notes, were grown in the "smut inheritance plot" to determine to what extent it was possible to isolate smut-resistant strains of corn under non-epidemic conditions, when the corn was grown under a systematic rotation, as compared to the reaction of these strains when grown in an artificially induced smut epidemic.

Thirty-four selfed lines which were being used as parent lines for single and double crosses in the plant breeding nursery, were grown in the smut inheritance plot in 1926 in order more accurately to test the manner of their reaction to smut. These strains were not selected because they were thought to be resistant to smut infection but because of their general desirability as parent lines for making crosses, as judged from several years' observations and notes, one of which was the note on smut infection.

Eight low smut strains, proved to be such under epidemic conditions, were combined in 1925 in order to determine whether the same genetic factors were concerned in determining resistance in all parent lines of such a combination. In making the combination, pollen was collected from seven of the eight strains, mixed, and used to pollinate the eighth strain, and so on until all the parent strains had been pollinated by a mixture of pollen of the other seven strains. The progeny of each female parent was grown separately in 1926.

During 1925 and 1926 a co-operative experiment was carried on by the sections of plant breeding and plant pathology at the University of Minnesota and the department of agronomy of the University of West Virginia. Ten selfed lines of corn from each experiment station, of known reaction in a smut epidemic, were exchanged and these twenty strains were grown at both experiment stations in 1925 and 1926. It was hoped that this would give an index to the reaction of different selfed lines under different environmental conditions and against, possibly, different physiologic forms of corn smut.

Selfed lines of corn with known genetic factors in one or more of the eight established chromosome linkage groups were also grown in the smut inheritance plot, for the purpose of determining their resistance or susceptibility to smut in order that they might be crossed with other selfed lines differing in smut reaction and one or more known genetic factors; and the presence or absence of linkage between factors determining smut reaction and these qualitative factors determined. It was hoped that the location of the factors determining resistance or susceptibility to smut might be established in one or more of the chromosome linkage groups and their inheritance more definitely determined. Crosses were made, therefore, between strains differing in these known genetic factors and in smut reaction. Six such crosses, involving nine different factor pairs, located in six different chromosome linkage groups, were made in 1924; and four more crosses, involving four more factor pairs and adding one more linkage group, were made in 1925. The F_1 crosses were grown in 1925 and 1926. The F_2 generation of the 1924 crosses was grown in 1926.

Seedling infection in the greenhouse was studied by hypodermically inoculating F_3 lines of seedlings grown from seed of forty-one F_2 plants selected at random from a cross of Rustler high × low smut lines. The same F_3 lines had been grown in the field in both 1925 and 1926. Seed of the same F_2 ears was used both years in the field as well as for the greenhouse test. A preliminary greenhouse test of the susceptibility of the seedlings from the parent lines gave inconclusive results, owing to the small number of plants involved. An insufficient amount of seed prevented the parent lines from being tested a second time.

The seeds were planted in sand in the greenhouse bench on December 16, 1926, in rows crosswise of the bench, sixteen seeds being planted per row and each culture replicated twice, that is, grown in three systematically distributed rows. The seeds were spaced 2 inches apart in rows 3 inches apart. On January 8, the seedlings were artificially inoculated with sporidia in carrot decoction, from a single physiologic form of *Ustilago zeae* obtained from Dr. Christensen. This physiologic form was originally isolated from a smut infection on a plant in a Longfellow low smut culture grown at University Farm.

The seedlings were inoculated by hypodermic injection of smut conidia into the plants in two places—the growing point of the plant and again about an inch higher. Notes were taken on both the place and the degree of infection of the individual seedlings, on one replicate on January 19 and on the other two replicates on January 21. In calculating the percentage of seedlings infected by smut in a given F_3 line, only those plants were considered as smutted which had developed definite smut boils (See Fig. 7). Plants with only small pimples on the leaves or chlorotic areas surrounding the point of inoculation of the leaves were not considered smutted.

EXPERIMENTAL RESULTS

In order to study the inheritance of resistance to smut, it was first necessary to isolate parent strains which were apparently homozygous for the factors determining a particular type of smut reaction. This homozygosity was reached by the method of selection in self-fertilized lines. Considering the apparent ease with which Hayes, et al (32), and Garber and Quisenberry (25) succeeded in isolating selfed lines of corn breeding true for a particular type of smut reaction, it appears that only a few main factors were involved in determining resistance. The manner of inheritance of these factors was unknown, however.

Each of the selfed strains and crosses in the smut inheritance plot was grown in two systematically distributed plots. The correlations between the percentage of total plants infected in the first and second series of these plots in 1924, 1925, and 1926 are given in Tables I, II, and III.

TABLE I

Correlation Between Percentage of Total Smut Infection in First and Second Series of a Uniform Replication in 1924

Percentage of total smut in second series	Percentage total smut in first series														
	3	10	17	24	31	38	45	52	59	66	73	80	87	94	Total
3	2	1	1												4
10	3	3	2	1					1						10
17	3	4		1	1	1									10
24			3	5	1										9
31		1	4	1	1		1					1			9
38	1			2	2	3	2			1					11
45						3	2	1	1						7
52	1						1	1							3
59						3	1	2							6
66							1		1						2
73									1	1	1	1			4
80										1	1				2
87											1	1			2
94									1					1	2
Total	10	9	10	10	5	10	8	4	5	3	3	3		1	81

$r = +0.7982 \pm 0.0272$

TABLE II

Correlation Between Percentage of Total Smut Infection in First and Second Series of a Uniform Replication in 1925

Percentage total smut in second series	2.5	8.5	14.5	20.5	26.5	32.5	38.5	44.5	50.5	56.5	62.5	68.5	74.5	80.5	86.5	92.5	98.5	Total
	Percentage total smut in first series																	
2.5	3		1			1												5
8.5		5				1												6
14.5	1	1		2	1	1	1											7
20.5		1	3	2	1	3	2				1							13
26.5			1			1	1		1	1	1							6
32.5		1		1	1		1	1			1							6
38.5				2			4					1	2					9
44.5				1		1	2	1	2		2							9
50.5				1		1	3	4			3	1		1		1		15
56.5					3	1	1	1	5	3		2						16
62.5					2		1		2	1		4	2		2			14
68.5							1		1	1	1	1	4		1	1		11
74.5											1	2	1		1	2		7
80.5							1			1	1		3	2	1	3		12
86.5											2	1		1	3	2	3	12
92.5														2	1		1	4
98.5												1			1	5	6	13
Total	4	8	5	9	8	10	18	7	11	7	13	13	12	6	10	14	10	165

$r = +0.8316 \pm 0.0162$

TABLE III

Correlation Between Percentage of Total Smut Infection in First and Second Series of a Uniform Replication in 1926

Percentage total smut in second series	2.5	8.5	14.5	20.5	26.5	32.5	38.5	44.5	50.5	56.5	62.5	68.5	74.5	80.5	86.5	92.5	98.5	Total
	Percentage total smut in first series																	
2.5	5	4	1															10
8.5	4	4	3	1	1													13
14.5	3	4	4	5	2	3	1		1									23
20.5	1	3	2	2		2	2											12
26.5		1	2	2	1			2	1									9
32.5			3	1	3		2	1		1								11
38.5		1	5		3	3	2	2			1							17
44.5				1	1	1		1	2		1							7
50.5		1	1		1	4	1	1	1	2								12
56.5				2		1	2	1	1	1	1	1		2		1		12
62.5			2	1	1	1	1	3										10
68.5							1	2	1	1	1	1		1				8
74.5									1			2		1				4
80.5							1			3	1	1	1	2				9
86.5							1					1				2		4
92.5										1					1			2
98.5														1			1	2
Total	13	18	23	15	13	15	14	13	8	9	5	6	1	7	1	3	1	165

$r = +0.7750 \pm 0.0210$

The correlation coefficients were high, as would be expected, indicating that the strains reacted in very nearly the same way when grown in different parts of the field.

The probable errors were calculated by the pairing method first suggested by Wood and Stratton (73).[4] This formula gives the probable error in percentage for the mean of the two plots of each strain systematically replicated.

The probable error for the average of several years was computed from the formula $\frac{1}{N}\sqrt{a^2 + b^2 \ldots . n^2}$ where N = the number of seasons in which the probable errors were obtained and a + b . . . . n represents the separate errors for each year.

The probable error in percentage of the mean of two plots systematically replicated, as calculated by the pairing method, was determined for the groups of strains with a percentage of infection between two arbitrary limits. The probable errors of each such class or group of selfed lines, in 1924, 1925, and 1926, and the number of pairs of strains in each class from which the probable error was calculated, are given in Table IV.

TABLE IV

Probable Error in Percentage of Smut Infection in Selfed Lines and Crosses Differing in Percentage of Smut Infection as Calculated by the Pairing Method

Percentage total smut in class	1924		1925		1926	
	Pairs in class	P.E. in per cent	Pairs in class	P.E. in per cent	Pairs in class	P.E. in per cent
0- 10	7	53.7	10	17.4	20	41.2
10- 20	14	26.9	8	20.4	28	17.9
20- 30	19	14.4	18	19.8	25	20.9
30- 40	9	14.0	11	10.0	28	19.8
40- 50	12	7.5	24	14.8	19	12.4
50- 60	9	10.1	26	9.9	16	11.0
60- 70	11	5.2	15	6.9	10	10.7
70- 80			19	5.4	13	7.8
80- 90	..	...	15	4.2	6	2.7
90-100	..	...	19	2.5		
0-100	81	17.1	165	10.5	165	18.4

The probable error is seen to decrease rapidly as the percentage of smut infection increases. The reason for this is readily observed. While the actual deviations from the means in the low smut strains is smaller than in the high smut strains, the percentage of deviation is far higher for the low than for the high smut strains. A high probable error for the low smut strains is to be expected because a deviation, even tho small, gives a high percentage of error. The probable errors for the entire experiment were 17.1, 10.5, and 18.4 per cent for the years 1924, 1925, and 1926. It is obviously unfair to use these average probable errors for all strains regardless of their percentage of smut infection, because such probable errors would be too lenient with the low smut strains and would have an opposite effect on the high smut strains. The smaller number of low smut strains in the 1925 test explains the low (10.5 per cent) average probable error for that year. The probable errors of the strains and crosses in the 1924, 1925, and 1926 tests were, therefore, calculated from the probable errors in per cent in the classes into which the strains fell, as given in Table IV. The probable errors for past years, when used, were those previously reported by Hayes, et al (32).

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[4] P.E. = $\frac{\frac{\Sigma\ (\text{dev. in } \%)}{n}}{\sqrt{N}}$ where Σ = summation, dev. in % = deviations in percentage of infection of each plot of a selfed strain or cross from the mean of both plots of that strain, n = the number of deviations in percentage, and N = the number of plots in each strain.

Reactions of Parent Strains and Crosses to Smut Infection

Eleven selfed lines of corn which seemed to be homozygous for a particular reaction to *Ustilago zeae* in a smut epidemic, were selected as parent strains to be used in making crosses for a study of the inheritance of smut reaction. The percentage of total and of ear smut infection on these parent lines from 1921 to 1926, inclusive, is given in Table V. Ear smut, being very important from an economic standpoint, was calculated separately.

TABLE V

PERCENTAGE OF TOTAL AND EAR SMUT INFECTION OF SELFED LINES OF CORN WHICH WERE USED AS PARENT LINES IN MAKING CROSSES

Variety	Cult. No.	Percentage of total smut						
		1921	1922	1923	1924	1925	1926	Average
Rustler	28	84.5	100.0	98.0	83.8	100.0	89.2	92.6 ± 3.6
do	38	28.5	2.5	12.1	33.4	42.3	41.7	26.8 ± 1.7
do	33	2.0	2.2	12.6	4.3	3.5	0.0	4.1 ± 0.5
Minn. No. 13	30	58.0	62.8	85.5	74.4	97.4	52.2	71.7 ± 2.9
do	31	14.0	40.0	21.8	29.4	47.7	48.2	33.5 ± 2.0
do*	17	10.5	65.6	14.0	...	...	...	....
Longfellow	41	73.0	83.7	65.9	...	95.7	79.5	79.6 ± 3.4
do	40	12.0	27.7	69.1	52.4	77.7	69.0	51.3 ± 2.5
do	42	65.0	84.0	67.1	27.3	27.1	17.4	48.0 ± 2.9
do	43	4.5	19.4	7.4	15.0	8.8	9.5	10.8 ± 1.1
King Phillip	39	58.0	84.0	97.5	...	100.0	78.0	83.8 ± 4.0
		Percentage of ear smut						
Rustler	28	11.2	21.3	28.0	5.6	26.0	15.2	17.9
do	38	14.4	0.0	4.0	8.0	7.7	18.1	8.7
do	33	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Minn. No. 13	30	32.0	26.6	16.8	36.5	26.2	10.9	24.8
do	31	0.0	4.0	4.5	0.0	3.1	7.4	3.2
do*	17	0.0	0.0	2.0	...	...	...	...
Longfellow	41	35.4	20.9	26.5	...	19.5	8.8	22.3
do	40	4.8	9.7	13.0	47.6	44.5	50.0	28.2
do	42	12.4	6.0	30.6	5.5	16.7	4.3	12.6
do	43	0.0	2.5	0.0	0.0	1.8	0.0	0.7
King Phillip	39	41.7	51.3	95.0	...	100.0	63.4	70.3

* Culture 17 was lost in 1923.

Eight of the strains gave nearly uniform results from year to year, indicating that the factors determining the particular type of smut reaction were in a practically homozygous condition. Cultures 17, 40, and 42 showed considerable variability.

Culture 17 was much more susceptible to smut in 1922 than in 1921 or 1923, 44.7 per cent of the infections in 1922 being due to tassel infection alone. Tassel infections were low in this strain in the other two years. Culture 42 had an average of 72.0 per cent of the plants infected by smut during the first three years of the test and only 23.9 per cent during the last three years. Apparently, the genotypic condition which determined the reaction of this strain from 1921 to 1923, inclusive, was not the same as that which determined its reaction from 1924 to 1926. The reverse was true with ear smut in culture 40. In this strain an average of 9.2 per cent of the plants were infected by ear smut during the period 1921 to 1923, and 47.3 per cent from 1924 to 1926. Culture 40 had a much higher percentage of smutted plants during the last four years of the test than during the first two years.

The relationship between total smut infection and amount of ear smut was not always constant, even within a variety. Cultures 40 and 42, in the variety Longfellow, had very nearly the same percentage of total smut for an average of six years, but twice as much ear smut was produced on culture 40 as on culture 42 during this period. The King Phillip culture, No. 39, had an extremely high percentage of ear smut. Since smut in corn is a pathological condition dependent on environmental conditions for dissemination of the spores and consequent chance for infection, some variability of infection is to be expected from year to year.

These parent lines were classified as high, medium, and low smut strains according to the average percentage of infection from 1921 to 1924, inclusive. Thus, the strains with an average of 0.0 to 15.0 per cent of total smut were classified as low smut strains; those with an average between 15.0 and 52.0 per cent were called medium smut strains; and those with an average of over 52.0 per cent infection were called high smut strains. Figure 3 shows the high smut strain of Rustler which was used in these crosses. While varying somewhat, the parent lines (except cultures 17, 40, and 42) were quite uniformly within these class limits from year to year. Culture 42 was a high smut line in the first three years of the test and a medium smut line in the last three years. In culture 40 there was a steady increase in ear smut infection from 1921 to 1926.

The F_1 crosses were grown in 1923 and again in 1924, when sufficient seed was available; 1922 seed was used both years. A summary of the percentage of total and ear smut infection in these F_1 crosses is given in Table VI.

TABLE VI

PERCENTAGE OF TOTAL AND EAR SMUT INFECTION IN F_1 CROSSES

Variety	Cult. No.	Type of smut reaction	Percentage total smut			Percentage ear smut		
			1923	1924	Av.	1923	1924	Av.
Rustler	28×33	High×Low	25.0	...	....	4.5	...	...
do	38×33	Med.×Low	3.0	2.6	2.8±0.8	0.0	0.0	0.0
Minn. No. 13 ...	30×17	High×Med.	45.1	46.5	45.8±3.9	12.5	22.1	17.3
do ...	17×31	Med.×Med.	8.6	32.5	20.6±2.2	0.0	6.5	3.3
Longfellow	43×42	Low×Med.	60.7	61.2	61.0±4.9	15.9	18.1	17.0
do	43×40	do	24.7	...	....	6.5	...	...

The percentage of total smut infection of the F_1 crosses was nearly the same for both years in three of the four comparable crosses; the percentages in 1923 and 1924 for the cross of lines 17 × 31 varied considerably. The difference between the results of the two years for this cross was five times its probable error. Such a large difference would be expected but once in 1350 trials on the basis of random sampling. In this cross, however, the 1923 data were obtained from only 35 plants grown in two systematically distributed rows, while the 1924 data were obtained from 77 plants grown in a single row.

The F_2 progenies were grown from seed of the selfed ears of the 1923 F_1 plants. The backcrosses of the F_1 with the parent strains were made in 1923 and the progenies were grown in 1924. In eight of the backcrosses it was possible to compare the percentage of smut infection of the progeny from crosses in which the F_1 was used as the male and as the female parent. That is, the F_1 was used as the staminate and as the pistillate parent in crossing back to either or both of the parent strains. A comparison of the percentage of smut found when the crosses were compared with their reciprocals is given in Table VII.

TABLE VII

COMPARISON OF PERCENTAGE OF TOTAL SMUT IN COMPARABLE CROSSES WHEN THE F_1 WAS USED AS THE STAMINATE AND WHEN USED AS THE PISTILLATE PARENT

Cross	Percentage total smut		F_1 as ♂ minus F_1 as ♀
	F_1 as ♂	F_1 as ♀	
Med. × High × High	74.0±3.9	74.3±3.9	− 0.3±5.5
Low × Med. × Med.	72.8±3.8	53.0±5.4	+19.8±6.6
Med. × Med. × High	55.0±5.6	45.2±3.4	+ 9.8±6.6
Med. × Med. × Med.	32.9±4.6	30.0±4.2	+ 2.9±6.2
do	22.8±3.3	22.5±3.2	+ 0.3±4.6
Low × Low × High	18.7±5.0	26.2±3.8	− 7.5±6.3
Low × Med. × Med.	9.6±5.2	10.8±2.9	− 1.2±6.0
Low × Low × Med.	9.5±5.1	6.1±3.3	+ 3.4±6.1

In only one of the eight crosses compared with its reciprocal was the difference as high as one and one-half times its probable error. In this one cross the difference was three times its probable error, which means that the odds were 22.6 to 1 that a deviation as great as the designated one or greater would be expected on the basis of random sampling. It may be concluded from these data that the factors for smut resistance or susceptibility were transmitted in the same manner in both male and female gametes.

In Table VIII is summarized the percentage of total and of ear smut infection in the parent lines and in the F_1, F_2, and backcrosses of these lines. The percentage of the parent lines and of the F_1 crosses is the average infection of these strains as given in Tables V and VI.

TABLE VIII

SUMMARY OF REACTIONS OF PARENT LINES, AND OF THE F_1 F_2, AND BACKCROSSES OF THESE LINES, TO ATTACKS OF *Ustilago zeae*

Variety	Parent line or cross	Type of smut reaction	Generation selfed or cross	Per cent total smut	Per cent ear smut
Minn. No. 13 ...	17	Medium	4	30.0 ± 4.2	0.7
do ...	31	do	7	33.5 ± 2.0	3.2
do ...	17 × 31	Med. × Med.	F_1	20.6 ± 2.2	3.3
do ...	17 × 31	do	F_2	26.2 ± 3.8	7.7
do ...	31 × (17 × 31)	Med. × (Med. × Med.)	Parent × F_1	32.9 ± 4.6	5.0
do ...	17 × (17 × 31)	do	Parent × F_1	22.8 ± 3.3	6.2
do ...	(17 × 31) × 31	(Med. × Med.) × Med.	F_1 × Parent	30.0 ± 4.2	3.8
do ...	(17 × 31) × 17	do	F_1 × Parent	22.5 ± 3.2	3.2
do ...	30	High	7	71.7 ± 2.9	24.8
do ...	17	Medium	4	30.0 ± 4.2	0.7
do ...	30 × 17	High × Med.	F_1	45.8 ± 3.9	17.3
do ...	30 × 17	do	F_2	52.2 ± 5.3	22.1
do ...	17 × (30 × 17)	Med. × (High × Med.)	Parent × F_1	55.0 ± 5.6	14.6
do ...	30 × (30 × 17)	High × (High × Med.)	Parent × F_1	74.0 ± 3.9	22.2
do ...	(30 × 17) × 17	(High × Med.) × Med.	F_1 × Parent	45.2 ± 3.4	9.3
do ...	(30 × 17) × 30	(High × Med.) × High	F_1 × Parent	74.3 ± 3.9	23.6
Rustler	28	High	7	92.6 ± 3.6	17.9
do	33	Low	7	4.1 ± 0.5	0.0
do	28 × 33	High × Low	F_1	25.0 ± 3.6	4.5
do	28 × 33	do	F_2	34.4 ± 4.8	11.1
do	33 × (28 × 33)	Low × (High × Low)	Parent × F_1	18.7 ± 5.0	6.3
do	(28 × 33) × 33	(High × Low) × Low	F_1 × Parent	26.2 ± 3.8	5.7
do	38	Medium	7	26.8 ± 1.7	8.7
do	33	Low	7	4.1 ± 0.5	0.0
do	38 × 33	Med. × Low	F_1	2.8 ± 0.8	0.0
do	38 × 33	do	F_2	12.9 ± 3.5	2.4
do	38 × (38 × 33)	Med. × (Med. × Low)	Parent × F_1	9.6 ± 5.2	1.9
do	33 × (38 × 33)	Low × (Med. × Low)	Parent × F_1	9.5 ± 5.1	2.4
do	(38 × 33) × 38	(Med. × Low) × Med.	F_1 × Parent	10.8 ± 2.9	0.0
do	(38 × 33) × 33	(Med. × Low) × Low	F_1 × Parent	6.1 ± 3.3	1.2
Longfellow	43	Low	7	10.8 ± 1.1	0.7
do	42	Medium	7	48.0 ± 2.9	12.6
do	43 × 42	Low × Med.	F_1	61.0 ± 4.9	17.0
do	43 × 42	do	F_2	47.5 ± 3.5	12.0
do	42 × (43 × 42)	Med. × (Low × Med.)	Parent × F_1	72.8 ± 3.8	22.8
do	(43 × 42) × 43	(Low × Med.) × Low	F_1 × Parent	22.4 ± 3.2	6.5
do	(43 × 42) × 42	(Low × Med.) × Med.	F_1 × Parent	53.0 ± 5.4	14.3
do	43	Low	7	10.8 ± 1.1	0.7
do	40	Medium	7	51.3 ± 2.5	28.2
do	43 × 40	Low × Med.	F_1	24.7 ± 3.5	6.5
do	43 × 40	do	F_2	16.8 ± 4.5	10.5
do	(43 × 40) × 43	(Low × Med.) × Low	F_1 × Parent	28.6 ± 4.1	5.8
do	(43 × 40) × 40	(Low × Med.) × Med.	F_1 × Parent	31.2 ± 4.4	31.5

In the Minnesota No. 13 medium × medium smut cross, the F_1 was slightly more resistant than the more resistant parent. If, however, the high percentage of tassel smut in culture 17 in 1923 (an abnormal condition) is eliminated, the F_1 was intermediate in reaction between the parents. The F_2 was slightly more susceptible than the F_1. In the backcross with culture 17 the percentages of total smut were lower than when backcrossed with culture 31. Culture 17 was the more resistant of the two parent lines of this cross.

In four of the other crosses the F_1 and F_2 gave an intermediate reaction between the parents. In the Longfellow low × medium smut cross, the medium smut parent was much more susceptible to smut infection the first three years of the test (1921-23, inclusive) than it was the last three years (1924-26, inclusive). The F_1 crosses were made in 1922 and the F_2 and backcrosses in 1923. The genotypic constitution of this parent strain was probably different when these crosses were made from that during the last three years of the test. This might account for the fact that the percentage of infected plants in the F_1 was higher than in the six-year average of either parent, and the F_2 reaction was as high as in the more susceptible parent.

The smut reaction in F_2 was very nearly the same as in F_1. In four of the six crosses the difference between the F_1 and the F_2 was less than twice its probable error and in all crosses the difference was less than three times its probable error.

In none of the backcrosses was the percentage of smut infection obtained significantly larger or smaller than that of either of the parents. In each of the nineteen backcrosses the reactions were intermediate, in twelve of the crosses being closest to that of the higher smut parent and in the other seven crosses most closely approaching that of the lower smut parent. In general, it can be concluded from these data that the smut reaction of the crosses was intermediate between the reactions of the parents.

In studying the inheritance of ear smut infection, it was found that in three of the six crosses the F_1 generation was more severely infected than the average of the parents; and in the other three crosses the F_1 was less severely infected than the average of the parents. In the F_2 generation seven of the eight crosses were more susceptible to ear smut infection than was the F_1. Of the nineteen backcrosses, ten were more severely infected with ear smut than either parent and the other nine gave an intermediate reaction, five of these being closest to the higher parent, one being the same as the average of the parents, and the other three crosses being closest to the lower parent.

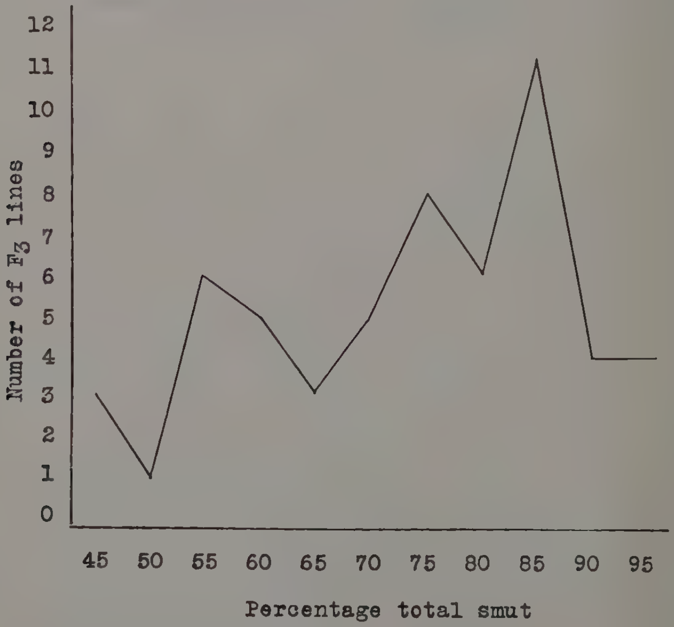
Corn smut, being due to a pathogene which is dependent on environmental conditions for dissemination of the inoculum and consequent chance for infection, and the percentage of infection consequently being quite variable, the inheritance of reaction of strains of corn to this organism can be best studied by self-pollinating a large number of F_2 plants selected at random and studying their nature by growing seed from them in the F_3.

In Table IX is graphically presented a summary of the reactions of 56 F_3 lines of the Minnesota No. 13 high × medium smut cross (30 × 17) grown in 1925. Unfortunately the medium smut parent was lost in 1923 and its reaction could not be compared with that of the F_3 lines grown in 1925.

TABLE IX

SUMMARY OF PERCENTAGE TOTAL SMUT IN F_3 LINES OF A MINN. NO. 13 HIGH × MEDIUM SMUT CROSS (30 × 17), GROWN IN 1925

The high parent had an average of 71.7 per cent smutted plants for an average of six years (97.4 in 1925) and the low parent had an average of 30.0 per cent smutted plants for an average of three years.



The range of variability of these F_3 lines exceeded the six-year average for the high smut parent but did not exceed the smut reaction of the high smut parent in 1925, the year the F_3 lines were grown. More of the F_3 lines resembled the more susceptible parent than the more resistant parent line, fifty-two being high smut lines while only four were medium smut lines in 1925, a very favorable year for a high degree of smut infection. The number of genetic factors involved can not be concluded from these data, however.

F_3 lines of another cross, that of Rustler high × low smut strains (28 × 33) were grown in both 1925 and 1926 from seed of the same F_2 plants. In Table X is shown the correlation between these F_3 lines when grown the two different years.

TABLE X

Correlation Between Percentage of Total Smut Infection of F_3 High × Low Smut Lines Grown in 1925 and 1926 from Seed of the Same 1924 Ears

Percentage total smut in 1925	Percentage total smut in 1926																
	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	Total
15		2	1	1													4
20		2	3				1										6
25		1	1			1				1							4
30		3			1												4
35	1				2	1	1										5
40				3	1	1	1										6
45		1					1	1	1								4
50			1		2		1	2								1	7
55						1				1		1					3
60	1								1	1							3
65					1	1											2
70									1				1				2
75							1										1
80									1								1
Total	2	9	6	4	7	5	6	3	4	3		1	1			1	52

$r = +0.5574 \pm 0.0654$

The magnitude of the correlation indicates the tendency for the F_3 lines to produce relatively the same percentage of total smut infection when grown in these two years, indicating that genetic factors determined the reaction to smut infection under the given environmental conditions.

In Table XI are graphically summarized the averages of the reactions of these F_3 lines for the two years they were grown.

The variability of the F_3 lines did not extend to the limits set by either of the parent strains. Forty-two of the F_3 lines were medium smut lines while the other ten were high smut lines, as an average of the two years they were tested. No low smut lines were found in the F_3 generation. As in Table IX, more of the F_3 lines resembled the susceptible than the resistant parent line. It would be difficult to conclude from the table how many factors were involved in determining resistance or susceptibility to smut infection. The nature of the distribution of these F_3 lines indicates that several factors were involved.

TABLE XI

Summary of Average Percentage Total Smut in F_3 Lines of a Rustler High × Low Smut Cross (28 × 33), Grown in 1925 and 1926

The high smut parent had 94.6 and the low smut parent 1.8 per cent of smut infected plants during the same two years.

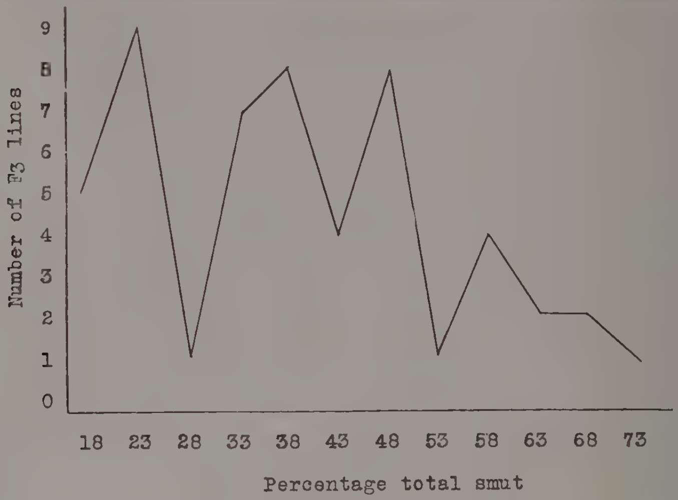
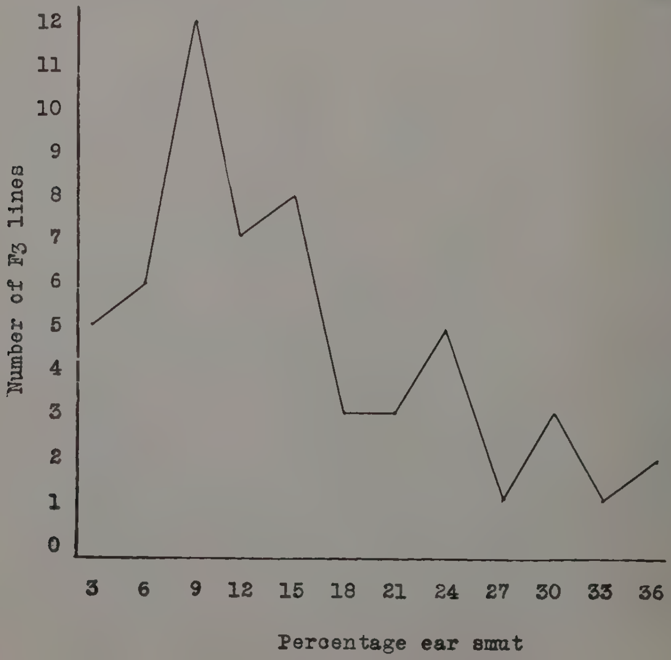


TABLE XII

Summary of Percentage Ear Smut in F_3 Lines of a Minnesota No. 13 High × Medium Smut Cross (30 × 17), Grown in 1925

The high parent had 24.8 per cent smutted ears for an average of six years (26.2 per cent in 1925), and the low parent had 0.7 per cent smutted ears for an average of three years.



The inheritance of reaction to ear smut infection was studied independently of total smut infection. The reaction of the F_3 lines of the Minnesota No. 13 high × medium smut cross (30 × 17) with regard to ear smut infection is shown in Table XII.

In this cross the distribution of the F_3 lines somewhat exceeded the limit set by the high smut parent. Thirty of the F_3 lines had less and twenty-six had more ear smut than the average of the parent strains.

TABLE XIII

Correlation Between Percentage of Ear Smut Infection of F_3 High × Low Smut Lines (28 × 33) Grown in 1925 and 1925 from Seed of the Same 1924 Ears

Percentage ear smut in 1925	Percentage ear smut in 1926																									
	0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5	12.5	13.5	14.5	15.5	16.5	17.5	18.5	19.5	20.5	21.5	22.5	23.5	24.5	Total
0.5	1		1		1		2			1																6
1.5	2		1					1	1																	5
2.5			1		1	1	1			1																5
3.5	2							1																		3
4.5				1			2	1								1	1									6
5.5					2																					2
6.5	2				1		1	1																		5
7.5	1				1																	1				3
8.5									1																	1
9.5	1	1		1																						3
10.5		1					1																			2
11.5				1						1																2
12.5					1																					1
13.5													1													1
14.5										1							1				1					3
15.5																										
16.5																										
17.5																										
18.5																										
19.5																										
20.5											1															1
21.5										1																1
22.5			1																							1
23.5																										
24.5																										
25.5																										
26.5																										
27.5																										
28.5																										
29.5																										
30.5																										
31.5																										
32.5																									1	1
Total	9	2	4	3	7	1	7	4	2	5	1		1			1	2			1	1				1	52

$r = +0.6311 \pm 0.0563$

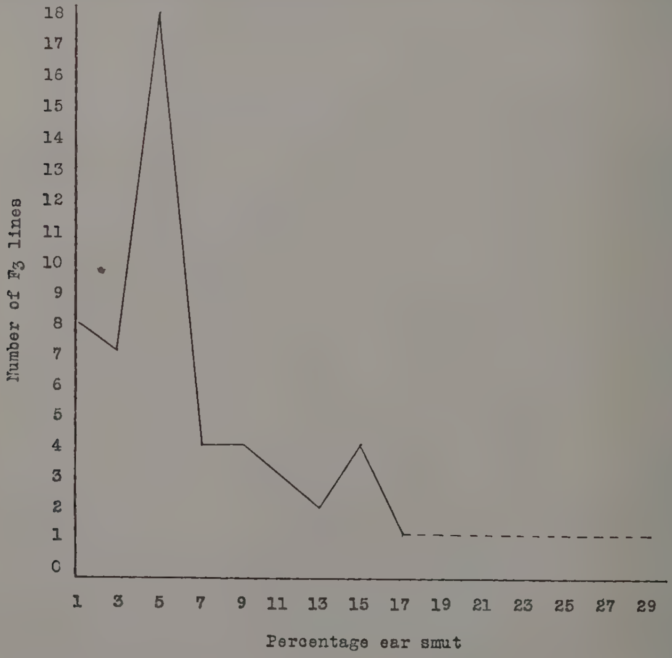
In Table XIII is shown the correlation between the percentage of ear smut infection of the different F_3 lines from the Rustler high × low smut cross (28 × 33) when grown from seed of the same F_2 ears in 1925 and 1926. The correlation coefficient of + 0.6311 ± 0.0563 indicates that genetic factors were here also involved in determining the reaction of these F_3 lines to ear smut infection in 1925 and 1926.

In Table XIV is shown the distribution of these F_3 lines with regard to the average percentage of ear smut infection for 1925 and 1926. In this cross, with the exception of a single F_3 line (29 per cent), none of the F_3 lines exceeded the limits of the parents. Forty-one of the F_3 lines had less and eleven had more ear smut than an average of the parent strains for the same two years.

TABLE XIV

SUMMARY OF AVERAGE PERCENTAGE EAR SMUT IN F_3 LINES OF A RUSTLER HIGH × LOW SMUT CROSS (28 × 33), GROWN IN 1925 AND 1926

The high parent had 20.6 and the low parent 0.0 per cent of ear smut for the same two years.



In general, the segregation in the F_3 lines with regard to total smut infection showed a higher percentage of susceptible than of resistant lines, when compared with the percentage of infected plants in the parent strains. The range of variability of the F_3 lines did not exceed the limits set by either parent. It seems, from these data, that it would be very difficult to obtain lines in F_3 which are as resistant as the more resistant parent of the cross. The number of genetic factors involved in determining resistance to smut infection could not be determined in these two crosses.

In the F_3 lines of crosses differing in percentage of ear smut, a greater number were more resistant to ear smut than the average of the parents in both of the crosses tested. In the high × low smut cross (28 × 33) the F_3 lines, with one exception, did not exceed the limits set by either parent. In the high × medium smut cross (30 × 17) seven of the fifty-six F_3 lines were more highly infected with ear smut than was the higher smut parent, indicating transgressive segregation in this cross.

Reactions of Selfed Lines Isolated in Regular Corn Breeding Nursery when Tested in Smut Inheritance Plot

Fifty-one selfed lines of corn, which had given a low percentage of infected plants in the regular corn breeding nursery, under normal field conditions, were tested for smut resistance in the smut inheritance plot, in order to determine the reliability of the selection of low smut strains in the regular corn breeding nursery, when the corn was grown under ordinary field conditions. Selfed lines of corn which are highly resistant to smut infection are very difficult to obtain at University Farm. The fifty-one selfed lines referred to were practically all of the strains growing in the regular corn breeding nursery which seemed to be highly smut-resistant under normal field conditions. These fifty-one selfed lines were selected from the selfed lines growing in the corn breeding nursery on the basis of the smut notes taken under normal field conditions over a period of years. They showed promise of being highly smut resistant and were consequently tested in the smut inheritance plot in order to be sure of their resistance. The results of this test are given in Table XV.

Of these fifty-one selfed lines of corn, which were practically all the lines resistant to smut infection under normal field conditions, twenty would be classified as low smut strains, twenty-six as medium smut strains, and five as high smut strains when grown in an artificially induced smut epidemic. Culture 32 is especially interesting because it was very resistant to smut infection for two years under normal field conditions but 100 per cent of the plants were infected by smut when grown in a smut epidemic. Of the seven strains with a percentage of ear smut infection of more than 10, five were in the medium smut group and two in the high smut group.

TABLE XV

PERCENTAGE OF SMUT INFECTION OF STRAINS OF CORN IN THE SMUT PLOT WHICH HAD GIVEN A LOW PERCENTAGE OF SMUT INFECTION FOR SEVERAL YEARS IN THE REGULAR CORN BREEDING NURSERY

Variety	1926 Cult. No.	Percentage total smut						Percentage ear smut		
		Smut plot			Regular breeding plots			Smut plot		
		1926	1925	1924	1923	1922	1921	1926	1925	1924
Rustler	29	80.0	82.4	71.0	0.0	10.0	22.0	7.3	13.2	7.9
N. W. Dent	32	100.0	100.0	100.0	2.0	0.0	39.0	40.0	28.1	12.5
Rustler	34	35.0	55.9	12.2	0.0	0.0	14.0	0.0	10.3	0.0
do	35	16.1	19.5	11.7	7.0	3.0	9.0	3.2	3.7	1.3
Minn. No. 13	36	16.3	20.0	2.0	0.0	0.0	...	2.0	7.1	0.0
N. W. Dent	37	5.1	8.5	4.1	0.0	3.0	37.0	0.0	0.0	0.0
Rustler	44	16.7	9.7	13.0	0.0	3.0	4.0	3.3	0.0	0.0
do	45	9.5	4.4	10.2	0.0	0.0	2.0	0.0	2.2	4.1
do	46*	...	38.0	24.6	0.0	6.0	10.0	...	8.0	3.1
Minn. No. 13	43*	...	89.2	26.3	0.0	0.0	4.0	...	6.5	13.2
do	74†	...	...	43.2	2.0	7.0	...	...	...	3.9
Rustler	80†	...	...	48.8	0.0	0.0	8.0	...	...	5.0
Longfellow	85†	...	...	40.0	7.0	3.0	65.0	...	...	22.0
King Phillip	86†	...	...	53.1	0.0	10.0	7.9	...	...	12.5
		(Smut plot)		(Regular breeding plots)						
Minn. No. 13	46	3.3	0.0	0.0	0.0	15.0	...	0.0	0.0	...
Rustler	47	7.9	8.9	0.0	0.0	0.0	14.0	0.0	1.8	...
do	48	2.3	9.3	3.0	0.0	0.0	7.0	0.0	2.3	...
Minn. No. 13	48*	...	29.0	0.0	3.0	0.0	...	...	5.3	...
do	49*	...	19.6	0.0	3.0	0.0	...	...	3.9	...
do	50*	...	25.5	0.0	0.0	0.0	...	...	0.0	...
do	51*	...	18.7	3.0	3.0	0.0	2.0	...	0.0	...
do	52*	...	47.8	0.0	0.0	0.0	4.0	...	8.8	...
Rustler	54*	...	33.3	0.0	0.0	3.0	4.0	...	22.2	...
King Phillip	56*	...	40.0	0.0	3.0	6.0	11.0	...	13.3	...
do	57*	...	39.1	0.0	3.0	3.0	4.0	...	8.8	...
Minn. No. 13	49	12.9	3.0	0.0	0.0	3.0	...	0.0	...	...
do	50	15.8	3.0	0.0	0.0	3.0	...	0.0	...	...
do	51	9.3	3.0	0.0	0.0	3.0	...	0.0	...	...
do	52	22.2	3.0	0.0	10.0	12.0	...	3.7	...	...
do	53	0.0	0.0	0.0	0.0	37.0	...	0.0	...	...
do	54	19.5	3.0	0.0	3.0	0.0	...	14.6	...	...
do	55	26.8	3.0	0.0	0.0	0.0	...	0.0	...	...
Rustler	56	5.6	0.0	5.0	6.0	...	...	0.0	...	...
do	57	34.7	0.0	0.0	5.0	...	...	12.2	...	...
do	58	30.9	0.0	0.0	8.0	...	...	0.0	...	...
do	59	46.0	0.0	12.0	2.0	...	...	2.7	...	...
do	60	10.8	5.0	3.0	5.0	0.0	4.0	0.0	...	...
do	61	32.1	3.0	4.0	3.0	3.0	18.0	7.2	...	...
Longfellow	62	13.2	8.0	0.0	7.0	1.0	...	5.3	...	...
Silver King	63	9.7	0.0	7.0	0.0	...	...	0.0	...	...
do	64	24.5	0.0	8.0	6.0	...	...	0.0	...	...
do	65	47.9	3.0	...	2.0	6.0	...	0.0	...	...
do	66	28.3	2.0	...	2.0	3.0	...	1.9	...	...
do	67	8.9	0.0	3.0	5.0	5.0	...	4.4	...	...
do	68	19.1	0.0	0.0	3.0	7.0	...	2.1	...	...
do	69	51.4	0.0	10.0	2.0	7.0	...	0.0	...	...
do	70	87.8	0.0	0.0	5.0	8.0	...	7.3	...	...
do	71	37.8	0.0	3.0	3.0	14.0	...	6.7	...	...
do	72	2.3	3.0	0.0	37.0	0.0	...	0.0	...	...
do	73	15.8	0.0	17.0	9.0	3.0	...	2.6	...	...
do	74	6.1	0.0	5.0	0.0	2.0	...	0.0	...	..

* 1925 culture numbers. † 1924 culture numbers.

Thirty-four selfed lines of corn which were being used as parent lines in making single and double crosses in the corn breeding nursery, were tested in the smut inheritance plot in 1926 in order more definitely to determine their reaction to smut infection. These strains were not selected necessarily because of their resistance to smut infection under non-epidemic conditions. They were considered to be the best available parent lines for single and double crosses, as judged by field observation and from notes, one of which was "percentage of smut infection." Some of these strains were known to be quite susceptible to smut infection but were selected because they were the best available, as judged by a large number of factors. The reaction of the thirty-four strains in an artificially induced smut epidemic is given in Table XVI.

TABLE XVI

SELFED LINES OF CORN, USED AS PARENT STRAINS IN SINGLE AND DOUBLE CROSSES IN THE REGULAR PLANT BREEDING NURSERY, TESTED FOR SMUT REACTION IN THE SMUT INHERITANCE PLOT IN 1926

Variety	Plant breeding 1926 Strain No.	Percentage smut	
		Total	Ear
Silver King	2	78.8 ± 6.1	12.7
do	6	52.4 ± 5.8	0.0
do	8	26.1 ± 5.5	0.0
do	1	67.4 ± 7.2	0.0
do	3	26.3 ± 5.5	10.5
do	4	34.0 ± 6.7	10.6
do	5	2.3 ± 0.9	0.0
do	7	25.0 ± 5.2	0.0
do	9	66.0 ± 7.1	1.9
do	10	47.9 ± 5.9	6.3
Minn. No. 13	11	12.7 ± 2.3	3.6
do	12	72.0 ± 5.6	4.0
do	13	15.4 ± 2.8	0.0
do	14	39.6 ± 7.8	20.8
Rustler	15	10.5 ± 1.9	0.0
do	16	75.6 ± 5.9	36.6
do	17	5.9 ± 2.4	0.0
do	18	64.6 ± 6.9	12.5
do	19	38.7 ± 7.7	2.3
do	20	11.1 ± 2.0	0.0
N. W. Dent	21	50.0 ± 6.2	9.4
do	22	55.8 ± 6.1	16.3
do	23	3.7 ± 1.5	0.0
do	24	34.7 ± 6.9	8.2
Longfellow	27	50.0 ± 6.2	26.1
do	26	25.5 ± 5.3	21.3
do	25	73.6 ± 5.7	5.9
do	28	71.5 ± 5.6	9.5
King Philip	29	78.3 ± 6.1	10.8
do	30	52.9 ± 5.8	9.4
Squaw	31	34.7 ± 6.2	16.3
do	32	34.2 ± 6.8	2.4
Dakota	33	35.1 ± 6.9	10.5
Red Flint	34	41.1 ± 5.1	28.6

Seven of these thirty-four strains would be classified as low smut strains, fifteen as medium smut strains, and twelve as high smut strains, in a smut epidemic, following the method of classification previously described.

It may be concluded from the data in Tables XV and XVI that selection of low smut strains of corn under normal field conditions is an aid in obtaining smut-resistant strains but that these strains should be tested in a smut epidemic in order to be sure of their resistance.

Combination of Eight Low Smut Strains

In 1925 a combination was made of eight strains of corn which seemed to be resistant to smut infection in a smut epidemic, in order to determine whether the factors for smut resistance were the same in all the eight strains and whether anything but low smut lines could be obtained in F_2 and later generations of such a combination.

It has been found, since this combination was made, that one of the eight parent strains was a medium smut strain while the other seven were low smut strains. In Table XVII are given the smut reactions of the F_1 combinations on each of the female parent lines as compared with those of the female parent lines grown the same year.

TABLE XVII

Smut Reactions of the F_1 Generation of a Combination of Eight Low Smut Selfed Lines Grown in 1926

Variety of ♀ parent	Cult. No.	Percentage total smut in		Percentage ear smut in	
		F_1 combination	♀ parent 1926	F_1 combination	♀ parent 1926
Rustler	165	22.6±4.7	0.0	6.5	0.0
do	166	10.6±1.9	35.0±6.9	2.1	0.0
do	167	7.3±3.0	16.1±2.9	0.0	3.2
Minn. No. 13 ..	168	18.0±3.2	16.3±2.9	6.0	2.0
N. W. Dent	169	5.4±2.2	5.1±2.1	1.6	0.0
Longfellow	170	7.3±3.0	9.5±3.9	0.0	0.0
Rustler	171	35.6±7.0	16.7±3.0	5.1	3.3
do	172	14.3±2.6	9.5±3.9	3.6	0.0
Average		14.9±2.7	12.4±2.2	2.9	1.1

None of the F_1 combinations were more susceptible to smut infection than were any of the strains used in making the recombination, when both were tested the same year. The average percentage of total smut infection (obtained by dividing the total number of plants infected by the total number of plants in the eight cultures) was not significantly different from the average percentage infection of the parent cultures. The average percentage of ear smut infection in the F_1 combination was only slightly higher than in the average of the parents. Apparently, the F_1 generation of a combination of low smut strains can be expected to be as resistant to smut infections as the average of the parents; as would be supposed from results obtained from F_1 crosses referred to in the discussion of the reactions of other F_1 crosses.

Location of Smut Boils on the Plants of a Strain

As has already been pointed out (25, 32, 36), the location of smut boils on the plants of a strain of corn is often characteristic of that strain. Further evidence of this was found in the selfed strains grown during the last three years. Thus, culture 74, grown in 1924, showed a peculiar location of smut boils on the necks of the plants (see Fig. 4). In this strain fourteen of the twenty plants infected had smut boils on the necks, that is, just below the tassel.

A brachytic strain, culture 8, grown in 1926, had leaf infections on twenty of the thirty infected plants in the culture. On the other hand, a Rustler strain, culture 38, had 33.4, 42.3, and 41.7 per cent of the plants infected in 1924, 1925, and 1926, respectively, but only one leaf infection during the three years. A Longfellow strain, culture 40, had 52.4, 77.7, and 69.0 per cent of the plants smutted during the same three years and but two leaf infections. On the other hand, the Silver King and Rustler cultures, 70 and 92, grown in 1926, had leaf infections on 67.0 and 72.0 per cent, respectively, of the infected plants.

Ear smut was a strain characteristic in the Longfellow culture 40, in which the percentage of total smut infection in 1924, 1925, and 1926 was 52.4, 77.7, and 69.0 per cent, respectively. Of the infected plants during this three-year period, 76.0, 59.0, and 91.0 per cent, respectively, showed ear smut infections. A strain of King Phillip, culture 39, had 100.0 and 78.0 per cent of the total plants infected by smut in 1925 and 1926, respectively. All infected plants in 1925 had smut infections on the ears. In 1926, 78.0 per cent of the infected plants had ear smut infections.

In 1925 two strains showed an extremely high percentage of tassel infection, and the stamens of one or more branches of the tassel became infected by smut. A Longfellow strain, culture 43, had 15.0, 89.1, and 9.5 per cent of its plants infected by smut in 1924, 1925, and 1926, respectively. The sugary-tunicate strain, culture 12, had 11.9, 95.4, and 12.2 per cent of its plants infected by smut during the same three years. The extremely high percentages of smut in 1925 in these two cultures were due largely to stamen infections. Eighty per cent of the infections of culture 43 and 90.0 per cent of the infections of culture 12 were attributable to tassel (stamen) infection alone in 1925.

A tassel seed strain, culture 10, grown in 1926, contained twenty-four ts_1 ts_1 plants, on which nineteen of the tassel ears were destroyed by smut. When these tassel ears were enclosed in a paper bag, in order to pollinate them artificially, they were practically always destroyed by smut and no seed could be obtained.

In the yellow endosperm strain, culture 5, infections at the base of the plants predominated. This strain showed smut boils on 56.6, 96.2, and 70.2 per cent of all the plants grown in 1924, 1925, and 1926, respectively. During these three years 70.0, 79.0, and 85.0 per cent, respectively, of the infected plants had smut boils at or near the base of the plants. Figure 5 shows base and lower ear bud infections on culture 6.

Infection of the rudimentary ear buds near the base of the plants or at the nodes between the ground and the developed ear (usually nearer the ground than the ear, are very common. This is particularly true late in the season when the plants have practically attained their full development. These shoots, or buds, containing meristematic tissue and being so located that the inoculum may fall or be washed over them, are very often infected by smut. The ear buds are also in a meristematic condition at a time when the temperature is usually high. This favors infection. Some strains are far more susceptible to infection at these locations than are others. For example, the Minnesota No. 13, culture 30, had smut boils on 74.4, 97.4, and 52.2 per cent of the plants in 1924, 1925, and 1926, respectively. Infections were found on the rudimentary ear buds of 50.0, 73.0, and 46.0 per cent of the infected plants during these three years. In the Rustler, culture 34, which showed 12.2, 55.9, and 35.0 per cent of total infection for the three years, 83.0, 68.0, and 90.0 per cent of the infected plants had ear bud infections. In the Northwestern Dent, culture 32, which had all plants infected by smut in 1924 and 1925, 88.0 and 78.0 per cent, respectively, of the infected plants had ear bud infections.

That the percentage of total number of plants infected, in a given strain, is not always an accurate index of its resistance or susceptibility, is shown by the fact that in the four strains having smut boils on more than 70.0 per cent of the plants in 1924, 1925, and 1926, 211 of the 430 smutted plants had more than one infection. In the four low smut strains with an average of less than 12 per cent of smutted plants, grown the same three years under the same conditions, only one of the forty infected plants had more than one smut boil. On plants of susceptible strains smut boils are usually larger than on infected plants of resistant strains. In the cultures mentioned above, 38.2 per cent of the infected plants in the high smut strains produced "large" smut boils and, of the remaining infected plants, 41.2 per cent had "medium" smut boils. Only 17.5 per cent of the infected plants in the low smut strains had large smut boils and of the remaining infected plants 25.0 per cent had medium smut boils.

A Co-operative Study of Smut Reaction Conducted by the Universities of Minnesota and West Virginia

During the seasons of 1925 and 1926, seed of ten selfed lines of corn of known smut reaction, from both Minnesota and West Virginia, was exchanged and seed of the same ears from these twenty selfed lines was planted at both experiment stations and the resulting plants were grown in a smut epidemic. It was expected that this experiment would give some evidence on the reaction of selfed lines of corn to smut infection under different environmental conditions as well as to probably different physiologic forms of corn smut.

In Table XVIII is given the percentage of total and of ear smut infections of these twenty selfed lines when grown at University Farm, St. Paul, Minnesota, and Morgantown, West Virginia, in 1925 and 1926.

TABLE XVIII

MINNESOTA AND WEST VIRGINIA SELFED LINES OF CORN GROWN IN BOTH STATES IN 1925 AND 1926

1926 Minn. Cult. No.	Description	Percentage total smut				Percentage ear smut			
		1925		1926		1925		1926	
		Minn.	W. Va.	Minn.	W. Va.	Minn.	W. Va.	Minn.	W. Va.
	MINNESOTA Selfed Lines								
28	High smut	100.0	62.5	89.2	74.7	26.0	28.2	15.2	25.3
29	do	82.4	26.1	80.0	29.1	13.2	7.2	7.3	0.0
31	Medium smut	47.7	13.6	48.2	8.6	3.1	0.0	7.4	5.2
33	Low smut	3.5	5.9	0.0	6.5	0.0	0.0	0.0	3.0
34	Medium smut	[illegible]	1.5	[illegible]	9.7	[illegible]	[illegible]	[illegible]	[illegible]
35	Low smut	19.5	18.3	16.1	24.4	3.7	1.4	3.2	15.1
36	do	20.0	15.9	16.3	1.6	7.1	0.0	2.0	0.0
37	do	8.5	2.9	5.1	1.0	0.0	0.0	0.0	1.0
39	High smut	...	...	78.0	85.7	...	...	63.4	78.6
41	do	...	...	79.5	9.8	...	...	8.8	2.0
30	do	97.4	18.3	...	...	26.2	1.7	...	...
32	do	100.0	66.7*	...	...	28.1	0.0*	...	...
	WEST VIRGINIA Selfed Lines								
18	Susceptible	98.0	61.5	...	33.3*	2.1	25.6	...	33.3*
19	Resistant	45.5	6.1	39.5	7.7	1.8	0.0	0.0	2.5
20	Susceptible	65.8	25.4	59.6	55.4	11.8	1.4	21.3	8.1
21	do	45.5	18.2†	...	...	13.6	0.0†	...	...
22	Resistant	58.0	10.3	15.9	2.2	16.0	0.0	0.0	2.2
23	do	23.4	1.5	25.0	2.0	0.0	0.0	0.0	0.0
24	do	9.0	0.0	3.9	1.1	0.0	0.0	0.0	1.0
25	Susceptible	92.0	66.7	100.0‡	53.8	34.0	4.4‡	25.0	23.1
26	Resistant	6.6	2.0	0.0*	0.0*	1.1	0.0*	0.0	0.0*
27	Susceptible	79.2	23.4	60.4	40.5	4.2	0.0	0.0	0.0

* 3 plants. † 11 plants. ‡ 4 plants.

A higher percentage of total smut infection was obtained in Minnesota than in West Virginia in all strains tested for two years. All strains which were smut-resistant in Minnesota were also resistant in West Virginia. Strains classed as medium smut lines in Minnesota were medium or low in West Virginia, and high smut strains in Minnesota were high or medium in West Virginia.

The location of smut boils on the plants of a culture, when grown in the two states the same year, was not the same in all instances. In culture 41, in which 79.5 per cent of the plants were infected in Minnesota and only 9.8 per cent in West Virginia in 1926, 47.0 per cent of the plants grown in Minnesota and only 2.0 per cent of those grown in West Virginia had smut boils at the base of the plants. In culture 30, in which the difference in percentage of total plants infected was 79.1 per cent in these two states in 1925, 88.0 per cent of the plants grown in Minnesota and only 7.0 per cent in West Virginia had infections on the main stalk and shoots. However, in this culture, 3.0 per cent of the plants grown in Minnesota and 10.0 per cent of those grown in West Virginia had basal infections.

In culture 18 the percentage of total smut infection was appreciably higher in Minnesota than in West Virginia, while the reverse was true of ear smut. In culture 27, smut infections at the base of the plants predominated in West Virginia in both years of the test, while infections on the main stalk predominated in Minnesota. The same condition was true in culture 32, grown in 1925.

A considerably higher percentage of the West Virginia selfed strains grown in Minnesota in 1926 had smut infections on the tassels than those grown in West Virginia the same year. The reverse was true in 1926. The corn was sprayed with a water suspension of smut conidia during its development in Minnesota, but not in West Virginia. This might account for the higher percentage of tassel smut in Minnesota in 1926. The Minnesota selfed lines had a higher percentage of tassel infection in Minnesota than in West Virginia in 1925. In 1926 some of these strains had an appreciably higher percentage of tassel infections in West Virginia, while in other strains the highest percentage of tassel infection was found in Minnesota.

In general, it may be concluded either that conditions for infection were slightly more favorable in Minnesota than in West Virginia or that the physiologic forms of smut encountered were more virulent in Minnesota than in West Virginia. Some selfed lines, when grown in both states from seed of the same ears, were attacked by smut to very nearly the same extent, while others were slightly more susceptible to infection in one state than in the other. The location of smut boils on the plants was not always the same in the two states in the same year. Smut infections on one location often predominated in one state while most of the infections were located on a different part of the plants in another state. This may have been due to the differential responses of the selfed lines to the probably different physiologic forms of smut. Environmental conditions may have been more favorable for infection in one state than in the other when specific parts of the plants were in a favorable condition for infection.

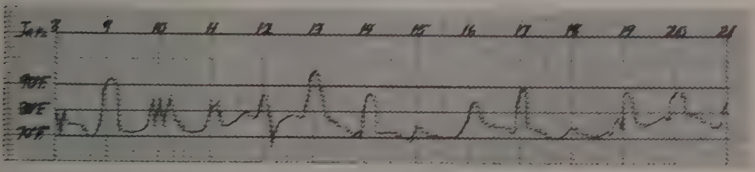
Seedling Infection in the Greenhouse

The same F_3 lines of the Rustler high / low smut cross (28 / 33) which were grown in the field in 1925 and 1926, were tested in the greenhouse for the purpose of studying their susceptibility to infection by a single physiologic form of smut. The purpose of this phase of the experiment was to determine the correlation between greenhouse and field notes on smut infection when both were obtained from plants grown from seed of the same ears.

The seeds of these F_3 lines were planted in sand benches in the greenhouse on December 16, 1926. The plants were inoculated hypodermically on January 8, 1927 (see Fig. 6). Notes were taken on January 19 and 21. Table XIX shows the range of temperature in the greenhouse between January 8, when the seedlings were inoculated and January 21, when the final notes were taken. Figure 7 shows some of the infected seedlings when the notes were taken.

TABLE XIX

Range of Temperature in Greenhouse Between Time of Inoculation and Taking of Final Notes



A high temperature seemed to be a far more important factor in determining smut infection than seedling vigor. There seemed to be little correlation between the amount of infection and the apparent vigor of the seedlings. Smut boils appeared first on the seedlings growing in the warmest end of the greenhouse bench, altho, the plants were much weaker at this end than at the cooler end of the bench.

In Table XX is presented graphically the range of variability in the percentage of infected seedlings in the F_3 lines. The data from which this graph was made are given in the summary, page 52.

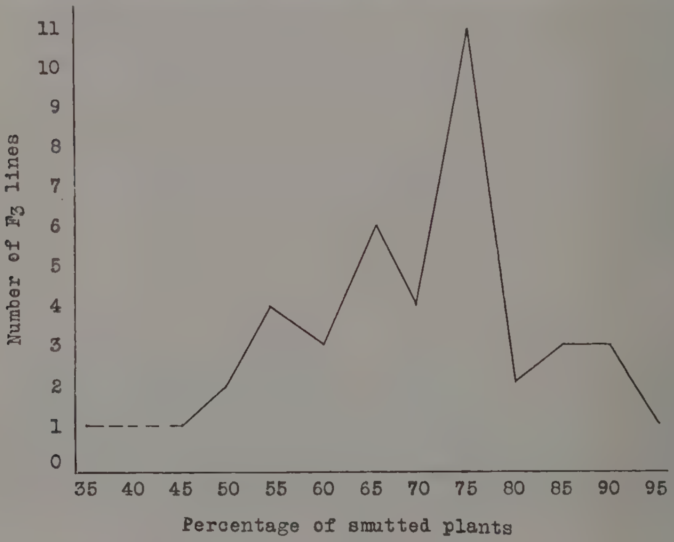
It may be concluded from Table XX that a high percentage of infected corn seedlings may be obtained by hypodermically inoculating with smut sporidia seedlings grown in sand in the greenhouse bench. A mean temperature of between 70° and 80° F. is sufficient for infection and development of smut boils.

There was some variability in the susceptibility of the F_3 lines of this cross to smut infection under the conditions of the experiment;

no lines were found, however, which showed an appreciable amount of resistance. It may be concluded from Table XX that some of the F_3 lines were more resistant than others to infection by this single physiologic form of corn smut, but the differences were not great, considering the small number of plants grown (22 to 48) from each F_3 line.

TABLE XX

SUMMARY OF PERCENTAGES OF SMUT-INFECTED CORN SEEDLINGS IN F_3 LINES OF A RUSTLER HIGH × LOW SMUT CROSS (28 × 33), GROWN IN GREENHOUSE AND ARTIFICIALLY INOCULATED WITH SPORIDIA OF A SINGLE PHYSIOLOGIC FORM OF SMUT



In Table XXI is shown the correlation between the percentage of infection obtained in the greenhouse when the seedlings were artificially inoculated, and the two-year average of infection obtained on the entire plants when grown in the field.

The correlation coefficient of +0.2854±0.1434 indicates a correlation of little significance between the percentages of seedling and field infection. Either conditions determining the amount of smut infection under field conditions were not the same as those in the greenhouse with seedlings hypodermically inoculated with a single physiologic form of smut, or the particular form of smut used was not able to differentiate the F_3 lines grown in the greenhouse in the same way as did the physiologic forms encountered under field conditions. In order to be of practical importance in determining the resistance to smut infection of selfed lines of corn grown in the greenhouse, a physiologic form, or forms, of smut would have to be found which would differentiate the strains in the same way in the seedling stage in the greenhouse as the forms found in the field did under field conditions.

TABLE XXI

Correlation Between Percentage of Seedlings Infected in Greenhouse and of Average Field Infection, Obtained from a Two-Year Test in the Field, of F_2 Lines from a Cross of Rustler High × Low Smut (28 × 33) Lines

Percentage of smutted plants in greenhouse	Average percentage smutted plants in field 1925 and 1926															
	18	22	26	30	34	38	42	46	50	54	58	62	66	70	74	Total
36				1												1
40																
44				1												1
48								1								1
52	1	1														2
56						1			1		1					3
60		1							2							3
64			1											1		2
68			2			1		2							1	6
72					1				1		1					3
76		3	2		2	1					1	1				10
80				1		1										2
84						1			1			1				3
88							1	1								2
92												1		1		2
Total	1	5	5	3	3	5	1	4	5		3	3		2	1	41

$r = +0.2857 \pm 0.1434$

Linkage Studies of Smut Reaction

It probably will be impossible to determine the number of genetic factors involved in determining reaction to smut infection until crosses are made and linkage relations determined between the factors determining smut reaction and other factors located in known chromosome linkage groups.

Sufficient material with known genetic factors located in different linkage groups is now available to enable the plant geneticist to determine which of the chromosome linkage groups in corn carry factors for such a quantitative character as smut resistance. It may not be possible, without very intensive study, to establish definitely how many factors are involved in determining reaction to corn smut, but the discovery of which of the ten chromosomes in corn carry factors for smut reaction will be a long step in the solution of this problem.

Corn normally has ten pairs of chromosomes. Eight chromosome linkage groups have been established. In Table XXII is presented a tentative map of the different chromosome linkage groups, showing the relative location of the genes and the distances between them. A number of genes are known to be carried in a particular chromosome, but their location has not been established in relation to more than one other factor in the chromosome. The last group of factors was, therefore, not placed on the chromosome map.

TABLE XXII

EIGHT ESTABLISHED LINKAGE GROUPS IN MAIZE WITH THE LOCI OF MANY OF THE GENETIC FACTORS ON THESE EIGHT CHROMOSOMES

Linkage group	Factors whose location has been determined	Location factors not yet determined	Literature citations
C	I pk C sh wx w_{11} d_3 v_1		4, 12, 14, 24, 34, 35, 66, 67
R	df pg_1 R l_1 g_1 w_2 li	de_2, Pr (?) gm_2, l_2	5, 14, 29, 44, 45, 46, 47, 51, 53, 69
su	su Tu	de, de_1 de_6 ge_1, v_8, wl	14, 22, 23, 39, 53, 70, 72
B	ts_1 v_4 B lg	sk	20, 21, 38
Y	w_5 Y w_6 Pl sm w_1	m_1, m_2	1, 11, 21, 50, 69, 70
P	br P ts_2	ad, f	2, 20, 41, 42
A	A v_3		71
Bn	v_5 gl Bn	pg_3, ra, Y_2, Yp	13, 29, 43

It is, then, with the factors in the above eight known linkage groups that the linkage relations of the factors determining smut reaction may be studied.

In Table XXIII are listed the genetic factors used in studying the linkage relations of the factors for smut reaction.

TABLE XXIII

FACTORS KNOWN TO BE LOCATED IN ONE OF THE EIGHT CHROMOSOME LINKAGE GROUPS AND USED IN STUDYING LINKAGE RELATIONS OF FACTORS FOR SMUT REACTION

(Dominant factors are capitalized.)

Factor	Character
A	Anthocyanin pigment (Emerson, 1918, 1921)
Bn	Brown aleurone (Kvakan, 1924)
br	Brachytic culms (Kempton, 1920)
g_1	Golden plant color (Lindstrom, 1918)
lg	Liguleless leaf (Emerson, 1912)
P	Pericarp color (Emerson, 1911)
Pr	Purple aleurone (East and Hayes, 1911; Emerson, 1918)
Pl	Purple plant color (Emerson, 1921)
R	Aleurone color factor (East and Hayes, 1911; Emerson, 1918, 1921)
sh	Shrunken endosperm (Hutchison, 1921)
sm	Salmon silk (Anderson, 1921)
su	Sugary endosperm (East and Hayes, 1911)
ts_1	Tassel seed (Emerson, 1920)
Tu	Tunicate ear (East and Hayes, 1911; Collins, 1917)
wx	Waxy endosperm (Collins, 1909)
Y_1	Yellow endosperm (East and Hayes, 1911)

Strains of corn carrying these genetic factors were used as parent lines in studying the linkage relations of the factors for smut reaction, and were grown in a smut epidemic to determine their resistance or susceptibility.

The percentage of total and ear smut infection of these strains with factors in known linkage groups is given in Table XXIV.

TABLE XXIV

SPECIAL STRAINS WITH GENETIC FACTORS IN KNOWN LINKAGE GROUPS

Characters and linkage groups	Strain No.	Percentage total smut			Percentage ear smut		
		1924	1925	1926	1924	1925	1926
Waxy endosperm (C), Pr tester (R ?)	1	10.0	22.2	15.8	0.0	4.4	0.0
Shrunken endosperm (C), purple (Y)	2	97.6	100.0	...	87.7	50.0	...
Sugary endosperm (su), tunicate (su)	3	11.9	14.2	12.2	2.4	9.3	4.9
Sugary endosperm (su), R tester (R)	4	30.0	78.2	48.5	16.7	46.9	9.1
Yellow endosperm (Y)	5	56.6	96.2	70.2	3.8	21.6	10.6
Yellow endosperm (Y), liguleless (B)	6	75.0	70.4	75.7	50.0	38.9	21.6
Yellow endosperm (Y), golden (R)	7	7.4	92.4	56.8	5.6	51.3	31.8
Tassel seed—ts_1 (B)	8	...	...	62.5	...	...	2.1
Tassel seed—ts_1 (B)	9	42.6	41.9	...	18.5	6.5	...
Tassel seed—ts_2 (P)	10	37.1	33.1	...	25.7	0.0	...
Brachytic (P)	11	...	...	69.8	...	...	7.0
"A" tester (A)	12	27.3	97.6	71.1	10.9	30.0	20.0
Brown aleurone (Bn)	13	...	66.0	53.6	...	20.8	0.0
Salmon silk (Y)	14	...	57.5	28.0	...	21.3	8.0
Slashed (?)	15	...	...	30.4	...	...	2.2
Rustler glossy (?)	16	...	...	64.0	...	...	8.0

It was from these strains that the parent lines for the linkage study crosses were chosen. Six crosses were made in 1924. The F_1 generations of these crosses were grown the following year. In Table XXV is summarized the percentage of total and ear smut infection of the parent strains and the F_1 crosses of these strains.

In the five crosses in which the F_1 could be compared with the parent strains grown the same year (1925), the F_1 was intermediate in percentage of plants infected in three of the crosses, approached the high smut parent in another, and was as severely infected as the higher smut parent in the one remaining cross. As for ear smut infection, resistance was slightly dominant in four of the F_1 crosses which could be compared with the parents grown the same year, while in the other cross the F_1 most nearly approached the high smut parent.

Four more crosses were made in 1925, involving still other genetic factors, located in linkage groups not dealt with in 1924, as well as factors in other loci of the same chromosomes involved in the 1924 crosses. A summary of the reaction of these crosses is given in Table XXVI.

TABLE XXV

Percentage Total and Ear Smut in Parent Strains and F_1 Crosses Made for Linkage Study, F_1 Grown in 1925

Cross of strains	Description of parent strains	Percentage total smut in parents			Percentage ear smut in parents			Percentage smut F_1 1925	
		1924	1925	1926	1924	1925	1926	Total	Ear
33 ×	Rustler, low smut	4.3	3.5	0.0	0.0	0.0	0.0	45.8 ± 6.8	1.4
2	Purple (Y) shrunken (C), high smut	97.6	100.0*	...	87.7	50.0	...	....	...
33 ×	Rustler, low smut	4.3	3.5	0.0	0.0	0.0	0.0	27.8 ± 5.5	10.8
4	Sugary (su), R tester (R) high smut	30.0	78.2	48.5	16.7	46.9	9.1	....	...
41 ×	Yellow endosperm (Y), high smut	...	95.7	79.5	...	19.5	8.8	79.5 ± 4.3	14.7
33	Rustler, low smut	4.3	3.5	0.0	0.0	0.0	0.0	....	...
33 ×	Rustler, low smut	4.3	3.5	0.0	0.0	0.0	0.0	41.0 ± 6.1	9.6
39	Red pericarp (P), high smut ...	...	100.0	78.0	...	100.0	63.4	....	...
31 ×	Minn. No. 13, medium smut	29.4	47.7	48.2	0.0	3.1	7.4	100.0 ± 2.5	5.9
11	Brachytic (P), high smut	...	...	69.8	...	...	7.0	....	...
36 ×	Minn. No. 13, low smut	2.0	20.0	16.3	0.0	7.1	2.0	70.0 ± 4.8	12.5
6	Liguleless (B), yellow endosperm (Y), high smut ...	77.0	70.4	75.7	50.0	38.9	21.6	....	...

* 2 plants.

TABLE XXVI

Percentage Total and Ear Smut in Parent Strains and F_1 Crosses Made for Linkage Study, F_1 Grown in 1926

Cross of strains	Description of parent strains	Percentage total smut in parents			Percentage ear smut in parents			Percentage smut in F_1 1926	
		1924	1925	1926	1924	1925	1926	Total	Ear
28 ×	Rustler, high smut	83.8	100.0	89.2	5.6	26.0	15.2	91.0 ± 2.5	32.5
3	Sugary (sh), tunicate (su), low smut	11.9	14.2	12.2	2.4	9.3	4.9	....	...
28 ×	Rustler, high smut	83.8	100.0	89.2	5.6	26.0	15.2	49.2 ± 6.1	9.5
1	Waxy (C), Pr tester (R ?), low smut	10.0	22.2	15.8	0.0	4.4	0.0	....	...
28 ×	Rustler, high smut	83.8	100.0	89.2	5.6	26.0	15.2	72.0 ± 5.6	30.7
7	Yellow endosperm (Y), golden (R), medium smut	7.4	92.4	56.8	5.6	51.3	31.8	....	...
9 ×	Ts_1 (B), high smut	42.6	41.9	...	18.5	6.5	...	15.2 ± 2.7	0.0
33	Rustler, low smut	4.3	3.5	0.0	0.0	0.0	0.0	....	...

The F_1 generation of the first cross, that of Rustler high smut × sugary, tunicate, low smut (28 × 3), was as susceptible to total plant infection as the most susceptible parent of the cross when both were grown the same year and more susceptible to ear smut infection. In the other three crosses the F_1 gave an intermediate percentage of total smut when compared with the parent strains. Two of the remaining three crosses were more susceptible to ear smut infection than was either parent, while resistance was dominant in the third.

Five of the six F_1 crosses made for linkage study in 1924 and grown in F_1 in 1925, were grown in F_2 in 1926. While grown in a plot apart from the other selfed lines, and the crosses being tested for smut reaction, they were grown in an artificially induced smut epidemic. Notes were taken on individual plants only once. Tables XXVII to XXXVII give the F_2 progenies of the various crosses involving possible linkages between the factors for smut reaction and known genetic factors in the linkage groups.

In Table XXVII are given the F_2 progenies of the cross low smut, normal endosperm × high smut, shrunken endosperm (33 × 2).

TABLE XXVII

F_2 PROGENIES OF CROSS LOW SMUT, NORMAL ENDOSPERM × HIGH SMUT, SHRUNKEN ENDORPERM (33 × 2)

Culture No.	Plants from seeds with normal endosperm			Culture No.	Plants from seeds with shrunken endosperm			Percentage plants smutted from	
	Smutted	Not smutted	Total		Smutted	Not smutted	Total	Normal seeds	Shrunken seeds
1, 13, 25	86	205	291	7, 19, 31	29	41	70	29.6	41.4
2, 14, 26	44	173	217	8, 20, 32	11	42	53	20.3	20.8
3, 15, 27	41	128	169	9, 21, 33	9	26	35	24.3	25.7
4, 16, 28	65	110	175	10, 22, 34	9	33	42	37.1	21.4
5, 17, 29	58	152	210	11, 23, 35	17	33	50	27.6	34.0
6, 18, 30	65	142	207	12, 24, 36	29	40	69	31.4	42.0
Total	359	910	1269		104	215	319	28.3	32.0

The difference between the total percentage of infected plants grown from seeds with shrunken and non-shrunken endosperms was only 4.3 per cent. Apparently there was no linkage between the factors for smut reaction and those for shrunken vs. non-shrunken endosperm carried in the "C" linkage group.

Two per cent of the plants grown from non-shrunken seeds had ear smut infections, and 1.9 per cent of those from shrunken endosperm seeds.

In Table XXVIII are summarized the F_2 data on the progenies of the low smut, white aleurone × high smut, purple aleurone cross (33 × 2). A total of 984 purple, 105 red, and 890 colorless seeds was obtained in F_2 and these were available for planting. Assuming two color factors, besides the Prpr factors, segregating for color, a 9:7 ratio of colored to colorless would be expected. The obtained segregation fits this expectation very well. The red seeds appear to be much too few for a 3:1 ratio of purple to red. Hayes and Brewbaker (29) suggested that this may be due to a linkage of the Prpr and Rr factors, the latter being carried in the "R" linkage group.

TABLE XXVIII

F$_2$ PROGENIES OF CROSS LOW SMUT, WHITE ALEURONE × HIGH SMUT, PURPLE ALEURONE (33 × 2)

Culture No.	Plants from seeds with white aleurone			Culture No.	Plants from seeds with red aleurone			Culture No.	Plants from seeds with purple aleurone			Percentage plants smutted from		
	Smutted	Not smutted	Total		Smutted	Not smutted	Total		Smutted	Not smutted	Total	White seeds	Red seeds	Purple seeds
1, 7	60	113	173	25, 31	5	10	15	13, 19	50	123	173	34.7	33.3	28.9
2, 8	25	101	126	26, 32	2	9	11	14, 20	28	105	133	19.8	18.2	21.1
3, 9	21	73	94	27, 33	2	7	9	15, 21	27	74	101	22.3	22.2	26.7
4, 10	30	77	107	28, 34	6	10	16	16, 22	38	56	94	28.0	37.5	40.4
5, 11	23	84	107	29, 35	3	7	10	17, 23	49	94	143	21.5	30.0	34.3
6, 12	36	89	125	30, 36	5	7	12	18, 24	53	86	139	28.8	41.7	38.1
Total	195	537	732		23	50	73		245	538	783	26.6	31.5	31.3

The greatest difference in percentage between smutted plants grown from white, red, and purple aleurone seed was 5.9. It can be concluded from these data that the factors for smut reaction are probably inherited independently of the Prpr factors.

The percentage of plants with ear smut infections was 2.1, 2.1, and 1.8 for the progenies of the white, red, and purple aleurone seeds, respectively.

In Table XXIX are summarized the F_2 data of the progenies of the low smut, starchy endosperm × high smut, sugary endosperm cross (33 × 4).

TABLE XXIX

F_2 PROGENIES OF CROSS LOW SMUT, STARCHY ENDOSPERM × HIGH SMUT, SUGARY ENDOSPERM (33 × 4)

Culture No.	Plants from seeds with starchy endosperm			Culture No.	Plants from seeds with sugary endosperm			Percentage plants smutted from	
	Smutted	Not smutted	Total		Smutted	Not smutted	Total	Starchy seeds	Sugary seeds
37	76	220	296	42	19	50	69	25.7	27.5
38	47	267	314	43	19	56	75	15.0	25.3
39	62	163	225	44	12	41	53	27.6	22.6
40	84	174	258	45	11	51	62	32.6	17.7
41	57	222	279	46	3	40	43	20.4	7.0
Total	326	1046	1372		64	238	302	23.8	21.2

The difference in percentage between the smutted plants grown from starchy and from sugary endosperm seeds was only 2.6. Apparently the factors for smut reaction and for sugary vs. starchy endosperm, located in the "su" linkage group were independently inherited.

The percentage of plants with ear smut infections was 2.6 and 3.3, respectively, for the plants grown from starchy and sugary endosperm seeds.

In Table XXX are summarized the F_2 data of the progenies of the cross (36 × 6) between low smut, ligulate plants × high smut, liguleless plants.

TABLE XXX

F_2 PROGENIES OF CROSS LOW SMUT, NORMAL PLANTS × HIGH SMUT, LIGULELESS PLANTS (36 × 6)

Culture No.	Normal plants			Liguleless plants			Percentage plants smutted	
	Smutted	Not smutted	Total	Smutted	Not smutted	Total	Normal	Liguleless
63, 67, 71	44	182	226	51	49	100	19.5	51.0
64, 68, 72	44	252	296	46	59	105	14.9	43.8
65, 69, 73	22	255	277	52	42	94	7.9	55.3
66, 70, 74	70	202	272	97	14	111	25.7	87.4
75	21	61	82	16	3	19	25.6	84.2
76	83	395	478	84	61	145	17.4	57.9
Total	284	1347	1631	346	228	574	17.4	60.3

In the progenies of each of the six F_1 ears, as well as in the total number of plants, is shown a distinct correlation between susceptibility to smut infection and liguleless plants. The difference in percentage between the normal and liguleless smutted plants was 42.9. Apparently the factor or factors for susceptibility to smut were linked in inheritance with the factors for ligulate vs. liguleless plants, located in the "B" linkage group.

The parent strains of this cross, grown in another plot in 1926, had 21.6 per cent of the liguleless and 2.0 per cent of the ligulate plants infected on the ears. In the F_2, 1.1 per cent of the ligulate plants had ear infections, and 0.9 per cent of the liguleless plants. The percentages were too small to allow any conclusions to be drawn from them, except that there seemed to be no linkage between ear smut and the Lglg factors. These plants matured very late in the season, which probably accounted for the low percentage of ear smut infection.

Smut infections on the base of the plants and on the ear buds predominated in the liguleless parent (see Fig. 5). Smut infections on this part of the plant also predominated in the liguleless plants in the F_2. Smut infections on the ligulate parent strain were not localized, as was also true in the ligulate plant segregates in the F_2.

Susceptibility to smut infection in this cross may have been closely associated with such morphological plant characters as the liguleless condition; it may have been a case of physiological susceptibility determined by genetic factors, or it may have been a combination of the two possibilities, that is, genetic linkage may have been involved in determining susceptibility in the liguleless plants with certain morphological characters of the liguleless plants markedly influencing the expression of the character smut susceptibility. It seems that in this case smut infection on the ear buds was strongly associated with the liguleless condition. Having no ligule, the inoculum could more easily fall upon or be washed over the ear buds in the liguleless plants than in normal plants, whose ear buds have more protection against inoculation. This might account for the susceptibility of the liguleless plants.

In Table XXXI are summarized the F_2 data on the progenies of the cross low smut, green plants × high smut, purple plants (33 × 2).

The difference in percentage between the purple and green smutted plants was only 1.7. Apparently the factors for smut reaction were not linked with the Plpl factor pair determining purple and green plants, located in the "Y" linkage group.

TABLE XXXI

F_2 PROGENIES OF CROSS LOW SMUT, GREEN PLANTS × HIGH SMUT, PURPLE PLANTS (33 × 2)

Culture No.	Purple plants			Green plants			Percentage plants smutted	
	Smutted	Not smutted	Total	Smutted	Not smutted	Total	Purple	Green
1, 7, 13, 19, 25, 31	85	188	273	30	58	88	31.1	34.0
2, 8, 14, 20, 26, 32	39	155	194	16	60	76	20.1	21.1
3, 9, 15, 21, 27, 33	33	123	156	17	31	48	21.2	35.4
4, 10, 16, 22, 28, 34	56	112	168	18	31	49	33.3	36.7
5, 11, 17, 23, 29, 35	54	130	184	21	55	76	29.3	27.6
6, 12, 18, 24, 30, 36	73	136	209	21	46	67	34.9	31.3
Total	340	844	1184	123	281	404	28.7	30.4

The purple plant parent of this cross was very susceptible to ear smut infection while the green plant parent was practically immune, under the conditions of the experiment. In F_2, 22 per cent of the purple plants had infected ears and only 9 per cent of the green plants.

In Tables XXXII, XXXIII, and XXXIV are summarized the F_2 data of the progenies of three different crosses between strains differing in smut reaction and color of endosperm.

TABLE XXXII

F_2 PROGENIES OF LOW SMUT, WHITE ENDOSPERM × HIGH SMUT, YELLOW ENDOSPERM CROSS (33 × 39)

Culture No.	Plants from seed with yellow endosperm			Culture No.	Plants from seed with white endosperm			Percentage plants smutted from	
	Smutted	Not smutted	Total		Smutted	Not smutted	Total	Yellow endosperm seeds	White endosperm seeds
47	86	158	244	52	17	57	74	35.2	23.0
48	68	147	215	53	16	49	65	31.6	24.6
49	64	148	212	54	13	48	61	30.2	21.3
50	76	157	233	55	17	49	66	32.6	25.8
51	61	186	247	56	22	42	64	24.7	34.4
Total	355	796	1151		85	245	330	30.8	25.8

TABLE XXXIII

F_2 PROGENIES OF MEDIUM SMUT, YELLOW ENDOSPERM × HIGH SMUT, WHITE ENDOSPERM CROSS (31 × 11)

Culture No.	Plants from seed with yellow endosperm			Culture No.	Plants from seed with white endosperm			Percentage plants smutted from	
	Smutted	Not smutted	Total		Smutted	Not smutted	Total	Yellow endosperm seeds	White endosperm seeds
57	50	36	86	60	19	24	43	58.1	44.2
58	115	101	216	61	38	31	69	53.2	55.1
59	100	121	221	62	25	18	43	45.2	58.1
Total	265	258	523		82	73	155	50.7	52.9

TABLE XXXIV

F_2 PROGENIES OF CROSS LOW SMUT, YELLOW ENDOSPERM × HIGH SMUT, WHITE ENDOSPERM (36 × 6)

Culture No.	Plants from seed with yellow endosperm			Culture No.	Plants from seed with white endosperm			Percentage plants smutted from	
	Smutted	Not smutted	Total		Smutted	Not smutted	Total	Yellow endosperm seeds	White endosperm seeds
63	76	172	248	67, 71	19	59	78	30.6	24.4
64	64	222	286	68, 72	26	89	115	22.4	22.6
65	53	225	278	69, 73	21	72	93	19.1	22.6
66	123	162	285	70, 74	44	54	98	43.2	44.9
Total	316	781	1097		110	274	384	28.8	28.6

The differences in percentages between the smut-infected plants in the F_2, grown from yellow endosperm seed and from white endosperm seed, in the three crosses summarized in Tables XXXII, XXXIII, and XXXIV, were 5.0, 2.9, and 0.2, respectively. Apparently the factors determining smut reaction and the Yy factor pair for yellow endosperm are not linked.

The percentages of plants having ear smut infections were 9.8 and 7.9 when the plants were grown from yellow and from white endosperm seed, in the first cross (Table XXXII). The percentages with ear smut infections were 2.5 and 1.9, respectively, in the second cross (Table XXXIII); and 0.6 and 1.3, respectively, in the third cross (Table XXXIV).

The factors Yy and Plpl are both located in the "Y" linkage group and are separated by a map distance equivalent to 29.7 per cent crossing over. Since the factors for smut reaction seem to be inherited independently of both the Yy and Plpl factors, which are located a considerable distance apart on the chromosome, the evidence indicates very strongly that the factors for smut reaction are not carried in the "Y" linkage group.

In Table XXXV are summarized the F_2 data of the progenies of the cross low smut, white pericarp × high smut, red pericarp (33 × 39).

TABLE XXXV

F_2 PROGENIES OF CROSS LOW SMUT, WHITE PERICARP × HIGH SMUT, RED PERICARP (33 × 39)

Culture No.	Plants with red pericarp			Plants with white pericarp			Percentage plants smutted with	
	Smutted	Not smutted	Total	Smutted	Not smutted	Total	Red pericarp	White pericarp
47, 52	55	130	185	7	62	69	29.7	10.1
48, 53	29	104	133	4	36	40	21.8	10.0
49, 54	36	113	149	2	47	49	24.2	4.1
50, 55	38	125	163	4	48	52	23.3	7.7
51, 56	23	142	165	8	51	59	13.9	13.6
Total	181	614	795	25	244	269	22.8	9.3

A distinct correlation is evident between smut reaction and pericarp color. More than twice as many of the plants with red pericarp ears were smutted as of plants with white pericarp ears. Apparently the factor, or factors, involved in determining smut reaction in this cross were linked with the Pp factor pair which determined pericarp color. The Pp factors are located in the "P" linkage group.

In this cross 7.2 per cent of the red pericarp plants had ear smut infections and only 2.6 per cent of the white pericarp plants. This is about the same ratio as was found in the case of total smut infection. The red pericarp parent had a very high percentage of ear smut infection (100 per cent in 1925 and 63.4 per cent in 1926) while the white pericarp parent was practically immune.

As no morphological demonstrable plant characters seemed to be associated with the factors for red pericarp color in this cross, that is, morphological characters which might be expected to influence the expression of smut reaction, it seems evident that genetic factors must here be responsible for the linkage between pericarp color and smut reaction.

Selfed strains of corn were found in the smut inheritance plot which all carried the red pericarp color factors (PP) and which varied in percentage of smut infection from 5.0 to 100.0. This suggests that the factors for pericarp color and for smut reaction could be linked in either the coupling or the repulsion phase.

In Table XXXVI are given the F_2 data of the progenies of the cross medium smut, normal plants × high smut, brachytic plants (31 × 11). In this cross twice as many of the brachytic as of the normal plants were infected by smut. Apparently the factor, or factors, determining smut reaction and the Brbr factors, determining the normal vs. brachytic plant characters, were linked in inheritance.

TABLE XXXVI

F_2 PROGENIES OF CROSS MEDIUM SMUT, NORMAL PLANTS × HIGH SMUT, BRACHYTIC PLANTS (31 × 11)

Culture No.	Normal plants			Brachytic plants			Percentage plants smutted	
	Smutted	Not smutted	Total	Smutted	Not smutted	Total	Normal	Brachytic
57, 60	42	57	99	27	3	30	42.4	90.0
58, 61	102	120	222	51	12	63	45.9	81.0
59, 62	76	131	207	49	8	57	36.7	86.0
Total	220	308	528	127	23	150	41.7	84.7

The brachytic parent strain had 7.0 per cent of ear smut in 1926 while the other parent strain had 7.4 per cent. In the F_2, 6.7 per cent of the brachytic plants had ear smut infections and only 1.1 per cent of the normal plants.

Smut infections on the main stalk predominated on the medium smut, normal plant parent. Infections on the leaves and ear buds predominated on the brachytic parent. In the F_2, ear bud infections were a trifle higher (37.3 per cent compared with 25.8 per cent) on the brachytic than on the normal plants. With regard to leaf infection, 32.0 per cent of the brachytic plants were infected and only 1.9 per cent of the normal plants. Of the brachytic plants, 22.6 per cent had main stalf infections in the F_2, while only 5.9 per cent of the normal plants had main stalk infections.

In this brachytic cross, susceptibility may have been determined by genetic factors for smut reaction, or morphological characters of the brachytic plants may have influenced the expression of smut susceptibility. Different parental lines were used in the red pericarp, high smut × white pericarp, low smut cross from those used in the brachytic plants, high smut × normal plants, medium smut cross. In the red pericarp color cross both parents carried the factors for non-brachytic (normal) plants. One of these parent lines was susceptible and one resistant to smut infection. The evidence, therefore, seems quite conclusive that genetic factors were involved in determining smut reaction in these two crosses.

As both the Pp and Brbr factor pairs, located in the "P" linkage group, seem to be linked with a factor or factors determining a specific reaction to smut infection, it may be concluded that factors determining smut reaction are carried in the "P" linkage group.

The parent strains of the cross low smut, white pericarp × high smut, red pericarp (33 × 39), grown in another plot in 1926, showed 0.0 and 78.0 per cent of infected plants in the white and red pericarp parents, respectively. The percentages of infected plants obtained in the F_2 progenies were 9.3 for the white pericarp plants and 22.8 for the red. This indicates that a certain amount of crossing over had occurred between the Pp factors and the factors for smut reaction. The parent strains of the cross medium smut, normal plants × high smut, brachytic plants (31 × 11) had 48.2 and 69.8 per cent of the normal and brachytic plant parent lines, respectively, infected by smut. In the F_2 of this cross, 41.7 per cent of the normal plants were infected and 84.7 per cent of the brachytic plants. It seems from these data that either a closer linkage exists between the factors for smut reaction and the Brbr factor pair than between the factors determining smut reaction and the Pp factor pair, or certain morphological characters of the brachytic plants influenced the amount of smut infection. If genetic factors alone were responsible for smut reaction, the genes would be in this order on the chromosome: pericarp color, smut reaction, brachytic plants; or pericarp color, brachytic plants, smut reaction.

In Table XXXVII are summarized the F_2 data of the progenies of a cross low smut, white aleurone × high smut, brown aleurone (36 × 6).

TABLE XXXVII

F_2 PROGENIES OF CROSS LOW SMUT, WHITE ALEURONE × HIGH SMUT, BROWN ALEURONE (36 × 6)

Culture No.	Plants from seeds with brown aleurone			Culture No.	Plants from seeds with colorless aleurone			Percentage plants smutted from	
	Smutted	Not smutted	Total		Smutted	Not smutted	Total	Brown aleurone seeds	Colorless aleurone seeds
67	15	47	62	71	4	12	16	24.2	25.0
68	16	71	87	72	10	18	28	18.4	35.7
69	20	51	71	73	1	21	22	28.2	4.5
70	32	37	69	74	12	17	29	46.4	41.4
Total	83	206	289		27	68	95	28.7	28.4

The percentages of smutted plants grown from brown aleurone and colorless aleurone seeds were almost identical, indicating that the genes for reaction to smut infection were inherited independently of the Bnbn factors, located in the "Bn" linkage group.

The percentage of plants with ear smut infections in F_2, was 1.7 for plants from brown aleurone seeds and 0.0 for plants from colorless aleurone seeds.

DISCUSSION AND CONCLUSIONS

Selfed lines of corn which seemed to be homozygous for factors determining a particular reaction to smut infection in an artificially induced smut epidemic, were selected as parent strains for making crosses for the purpose of studying the inheritance of smut reaction. It was possible to isolate strains which were practically homozygous for a particular type of smut reaction by selfing for only two or three years. In two of the parent lines used in these crosses, however, it was necessary to self for four or five years before they apparently became homozygous for the factors determining their reaction to smut infection. A uniform percentage of smut-infected plants for three years did not always furnish a reliable guide as to the reaction of these strains in subsequent years. The high correlations between the results obtained from the two series of a uniform replication, as well as the uniform results obtained from year to year, indicate that genetic factors were involved in conditioning a particular type of smut reaction.

Four different F_1 crosses were grown in two different years from seed of the same F_1 ears. Three of these crosses gave practically identical percentages of smut-infected plants in both years. The difference between the reactions of the fourth cross for the two years it was tested was five times its probable error. This difference may have been due to chance variability or it may have been caused by different physiologic forms of *Ustilago zeae* differentiating this cross for the two years of the test.

In eight backcrosses, in which the crosses could be compared with their reciprocals, the differences were all less than three times their probable errors, indicating that the factors were inherited alike in both male and female gametes.

In sixteen F_1 crosses, the reactions to total smut infection of the F_1 were intermediate in twelve crosses, approached the more resistant parent in one cross, and the more susceptible parent in the other three crosses. In six F_2 crosses which could be compared directly with the F_1, the percentage of smutted plants in F_2 was higher in four crosses and lower in two crosses than it was in the F_1. In nineteen backcrosses, twelve approached the more susceptible parent in reaction and seven approached the more resistant parent in percentage of infected plants.

Two crosses were tested in F_3 by growing a large number of F_3 lines from seed of selfed F_2 plants selected at random. In one of these crosses, that of Minnesota No. 13 high × medium smut (30 × 17), the percentage of smutted plants was intermediate in the F_1, slightly higher in F_2 than in F_1, the four backcrosses were as susceptible as the more susceptible parent, and in the F_3 there was found a large preponderance of high over medium smut lines. No F_3 lines exceeded the parents in percentage of smutted plants. In the other cross, that of Rustler high × low smut lines (28 × 33), in which resistance was slightly dominant in the F_1, the F_2 was slightly more susceptible than the F_1, one backcross was intermediate and the other was as susceptible as the more susceptible parent, the F_3 lines were all medium or high smut lines, no low smut lines being found in F_3. None of the F_3 lines exceeded the reactions of either parent.

In general, in these crosses, there was no dominance of either resistance or susceptibility in F_1; a majority of the F_2 and backcrosses varied in reaction, with a slight tendency for the backcrosses to approach the more susceptible parent; and in F_3 a preponderance of the lines approached, altho they did not exceed, the more susceptible parent in percentage of smut-infected plants.

With regard to ear smut infection, twelve of the sixteen F_1 crosses were intermediate, two approached the resistant parent in reaction, and two approached the more susceptible parent in percentage of ear smut. Five of the six F_2 crosses, which could be compared directly with the F_1, were more susceptible to ear smut infection in the F_2 than they were in the F_1, while the remaining F_2 cross was lower than the F_1. Thirteen of the nineteen backcrosses were intermediate in reaction and the other six were as susceptible as the more susceptible parent. In one of the crosses tested in F_3, in which the F_1 was intermediate, the F_2 was more susceptible than the F_1, and the four backcrosses were intermediate; about half of the F_3 lines were lower and the rest were higher in percentage of ear smut infection than the average of the parents. Seven of the F_3 lines were more susceptible to ear smut than the more susceptible parent. In the other cross tested in F_3, in which resistance to ear smut was slightly dominant in the F_1, the F_2 was more susceptible than the F_1, the backcrosses were almost as susceptible to ear smut infection as the more susceptible parent, forty-one of the F_3 lines were lower and eleven were higher in per cent of ear smut than the average of the parent lines—none of the F_3 lines in this cross exceeded the limits of the parent lines.

In general, the reactions to ear smut infection in these crosses were intermediate in F_1, the F_2 was slightly more susceptible than the F_1 in five of the six crosses, the backcrosses were either intermediate or approached the more susceptible parent in reaction, and slightly more than half of the F_3 lines were more resistant than the average of the parents. The F_1, F_2, and backcrosses were grown the same year, while the F_3 lines were grown in later years. In general, ear smut infection seemed to be inherited in the same way as total smut infection.

A large number of selfed lines of corn which had been grown for several years in the regular corn breeding nursery, were tested in the smut inheritance plot in an artificially induced smut epidemic, in order to determine the reliability of notes taken under normal field conditions, compared with smut epidemic conditions. In general, it was found that notes taken under average field conditions were an aid in obtaining smut-resistant strains, but that these strains should be tested in a smut epidemic in order to be sure of their resistance. If the strains to be so tested have been self-fertilized for three or four years, one year's test in a smut epidemic should give a relatively accurate index as to the actual resistance of the strain. Of the thirteen lines which had been selfed for at least four years and selected as being resistant under normal field conditions, the conclusions based on one year's test in a smut epidemic would have been erroneous in the case of two of these strains, as determined from results obtained by longer tests under epidemic conditions. These two strains probably were not homozygous for the factors determining smut resistance when first tested in the smut inheritance plot.

A combination was made of eight strains which seemed to be smut-resistant, in order to determine whether any lines not smut-resistant would be found in F_2 and later generations of the cross; or if the same genetic factors determined resistance in each of the eight strains combined. The average percentage of total and of ear smut infection was not significantly higher in the F_1 of the combinations than in the average of the parents grown the same year, as might be expected from results obtained in other F_1 crosses. Very nearly the same percentage of smut-infected plants was found in the female parent strains of the Minnesota No. 13, Northwestern Dent, and Longfellow varieties as in the F_1 combinations on these strains. However, considerable variability was found between Rustler female parent strains and the F_1 combinations on these strains. The number of parent strains was too small to allow any conclusions to be drawn from these facts.

A co-operative study was carried on with the department of agronomy of the University of West Virginia in which seed of ten selfed lines of corn of known smut reaction in a smut epidemic, from each state, were exchanged and grown at both Morgantown, West Virginia, and University Farm, St. Paul, in 1925 and 1926. In general, a higher percentage of smut-infected plants was obtained at University Farm than at Morgantown. The same general relationship between the percentage of infected plants in these two localities held for practically all strains involved in the test. Some of the strains were far more severely infected in Minnesota than in West Virginia, indicating either that different physiologic forms of smut were involved or that conditions for infection were more favorable in Minnesota than in West Virginia. The location of the preponderance of smut infections on the plants was not always the same when these strains were grown in both states the same year. As meristematic tissue is necessary for infection by the smut-producing organism, the differences in location of the preponderance of smut boils on the plants of some of the strains may have been due to the fact that environmental conditions necessary for infection were different when specific parts of the plants grown in these two states were most susceptible. Or the physiologic forms of smut encountered in the two states may have differed in their ability to attack specific parts of the corn plants.

The location of smut boils was shown to be a strain characteristic. Strains were found in which infections predominated on leaves, ears, tassels, base, rudimentary ear buds, and necks of the plants. Leaf infections predominated in the brachytic strain, which has a very high leaf area considering the size of the plants. Basal and lower ear bud infections predominated in a liguleless strain, which had less protection against the inoculum washing down behind the leaf and resulting in infection of the ear buds. A very large percentage of the tassel ears in a tassel seed strain were infected by smut. This strain, with its mass of exposed silks at pollination time, is admirably suited for infection at this point. These observations might suggest that the location of smut boils on the plants may be associated with certain morphological characters of the plants.

One of the Minnesota No. 13 strains, on the other hand, had a very large percentage of the infections located on the necks of the plants, while other strains of the same variety had no neck infections. Strains of the variety Rustler were found in which a high percentage of the plants had leaf infections while in other strains of the same variety leaf infections were extremely rare. One strain of Silver King also had a high percentage of leaf infections while in other strains the percentage was small. A selfed strain of Longfellow flint had practically no leaf infections but a high percentage of ear infections. Infections on the ear buds predominated in strains of four different varieties—Minnesota No. 13, Rustler, Northwestern Dent, and a yellow endosperm, liguleless strain—in which no morphologically demonstrable characters were apparent which could be considered as associated with the location of smut boils on the plants. While morphological characters of the plants may be associated with the location of smut boils on specific parts, resistance or susceptibility to smut infection at these locations may also be physiological.

Susceptible selfed strains of corn have a greater tendency toward multiple infections on the plants than have resistant strains. There was also a tendency for smut boils to develop to a greater size on susceptible than on resistant strains.

That the mere "percentage of smut-infected plants" in a given strain, without regard to the location of smut boils on the plants, may lead to erroneous conclusions, was shown in several instances. Three smut-resistant strains have been found which showed an extremely high percentage of infected plants in only one of several years in which they were tested. Upon checking the notes on the location of smut boils on the plants during this year, it was found that in each of the three cases this exceptional increase was due to tassel infection. This occurred but once in each of the three strains referred to, in several years. It would be quite possible to draw erroneous conclusions regarding the degree of resistance of these strains if this factor of the location of smut boils were not taken into consideration.

Seedlings of F_3 lines of a Rustler high × low smut cross (28 × 33) were grown in the greenhouse and inoculated hypodermically with smut sporidia of a single physiologic form of *Ustilago zeae*. It was found possible to obtain a high percentage of smut infections on seedlings grown in sand in a greenhouse bench with a mean temperature of between 70° and 80° F. Some variation was found in the amount of infection in these F_3 lines, but no lines with an appreciable degree of resistance were found. No significant correlation, as measured by the correlation coefficient, was found between seedling infection by a single physiologic form of smut, in the greenhouse, and plant infections under field conditions. Either conditions for seedling infection were different from those for plant infections in the field, or the physiologic form of smut used was not able to differentiate these F_3 lines in the same way as were the forms of smut encountered under field conditions.

Crosses were made between selfed strains of corn which differed in smut reaction as well as in genetic factors known to be located in one of the chromosome linkage groups. The linkage relations between the factors determining smut reaction and these other factors were then studied in the F_2 generation.

The factors determining smut infection were found to be inherited independently of the factors for shrunken vs. normal endosperm located in the "C" linkage group, the Prpr aleurone color factors which may be located in the "R" linkage group, the factors for sugary vs. starchy endosperm in the "su" linkage group, the factors for purple vs. green plant color, and the factors for yellow vs. colorless endosperm, both of which are in the "Y" linkage group, and the factors for brown vs. colorless aleurone located in the "Bn" linkage group.

The factors for smut reaction were found to be linked in inheritance with the factors for liguleless vs. ligulate plants located in the "B" linkage group and the factors for brachytic vs. normal plants and red vs. colorless pericarp, both of which are located in the "P" linkage group.

Because of unusual weather conditions in 1926 and the lateness of maturity of these F_2 crosses, the percentage of ear smut was low. However, in the crosses in which the parent strains differed markedly in percentage of ear smut infection, the F_2 segregates showed about the same linkage relations with regard to ear smut as they did with regard to total plant infection.

In the cross of the high smut, liguleless line × the low smut, normal line (36 × 6), infections on the base and lower ear buds predominated in the liguleless parent strain. The same condition was true of the liguleless plant segregates in the F_2. In the cross of the high smut, red pericarp line × the low smut, colorless pericarp line (33 × 39) there was no particular localization of smut boils on the red pericarp parent. There was a slight preponderance of infections on the ear buds and ears of the red pericarp plant segregates in the F_2. In the cross of the high smut, brachytic line × the low smut, normal line (31 × 11), infections on leaves, tassels, and ear buds predominated on the brachytic parent while main stalk infections predominated on the normal parent. In the F_2, infections on the ear buds, leaves, and main stalk predominated on the brachytic plant segregates, while infections on the ear buds, neck, and main stalk predominated on the normal plant segregates.

In the above three crosses there seemed to be some association between the location of smut boils on the plants of the parent strains and on the F_2 segregates of the crosses. There were, however, several instances in which a large percentage of smut boils on a specific location on the plants of one parent was associated with the opposite genotypic type of plants in the F_2. Because of conditions under which the parent strains and the F_2 crosses were grown in 1926, however, it would be difficult to draw definite conclusions regarding the extent to which location of smut boils on the plants of a parent strain was associated with the particular type of plants in the F_2.

SUMMARY

1. Inheritance of reaction to smut *(Ustilago zeae)* was studied in selfed lines of corn and crosses between these selfed lines.

2. Selfed lines of corn which were apparently homozygous for a particular type of smut reaction were isolated after only a few years of selfing.

3. Factors determining smut reaction were transmitted alike in both male and female gametes.

4. Crosses between selfed lines differing in smut reaction were, in general, intermediate in reaction. There were several cases of apparent dominance of susceptibility, however. A slight tendency to approach the more susceptible parent was found in the F_3 and back-crosses. Reaction to ear smut infection was inherited in the same manner as reaction to total smut infection.

5. Selection of selfed lines of corn resistant to smut under average field conditions was found to be an aid in obtaining such resistant strains, but they should be tested in a smut epidemic in order to be sure of their resistance.

6. F_1 combinations of eight smut-resistant strains were as resistant as the average of the parent strains.

7. The relationship between the percentage of smut-infected plants was quite constant for the same strains grown both in Minnesota and in West Virginia the same two years. The location of smut boils on the plants differed somewhat when grown in the two states. This may have been due to different physiologic forms of smut or to the fact that conditions for infection at different stages of the growth of the plants were not the same.

8. Location of smut boils on the plants was found to be a strain characteristic. Morphological characters of the plants may have been associated with the location of smut boils on the plants or physiologic susceptibility may have determined their location.

9. Seedling infection was studied in the greenhouse. No appreciable correlation was found between the amount of seedling infection with a single physiologic form of smut and plant infection under field conditions.

10. Linkage relations were studied between the factors determining smut reaction and one or more known genetic factors in seven of the chromosome linkage groups. The factors for smut reaction were found to be inherited independently of the Shsh, Prpr, Susu, Plpl, Yy, and Bnbn factor pairs, which are located in five different linkage groups, and to be linked with the factor pairs Lglg, Brbr, and Pp, which are located in two different linkage groups.

SUMMARY OF REACTIONS OF F_3 LINES OF RUSTLER HIGH × LOW SMUT CROSS (28 × 33)

The seedlings were grown in the greenhouse and artificially inoculated with sporidia of a single physiologic form of smut.

1926 Culture No.	No. of plants	Per cent smutted	1926 Culture No.	No. of plants	Per cent smutted
109	32	53.1	138	34	61.8
110	41	36.6	139	33	87.9
111	38	44.7	140	34	76.5
112	42	85.7	141	31	77.4
113	35	60.0	142	34	70.6
114	43	55.8	143	46	76.1
115	39	66.7	144	35	74.3
119	41	58.5	145	45	51.1
116	37	48.6	146	40	85.0
117	35	68.6	147	33	78.8
118	33	66.7	148	40	77.5
120	36	66.7	150	41	92.7
121	40	72.5	151	44	88.6
122	35	85.7	153	44	75.0
123	35	57.1	156	44	77.3
126	36	55.6	157	38	65.8
127	30	66.7	158	48	77.1
124	22	68.2	159	44	77.3
128	35	80.0	160	43	74.4
133	31	90.3	162	44	72.7
136	25	64.0			

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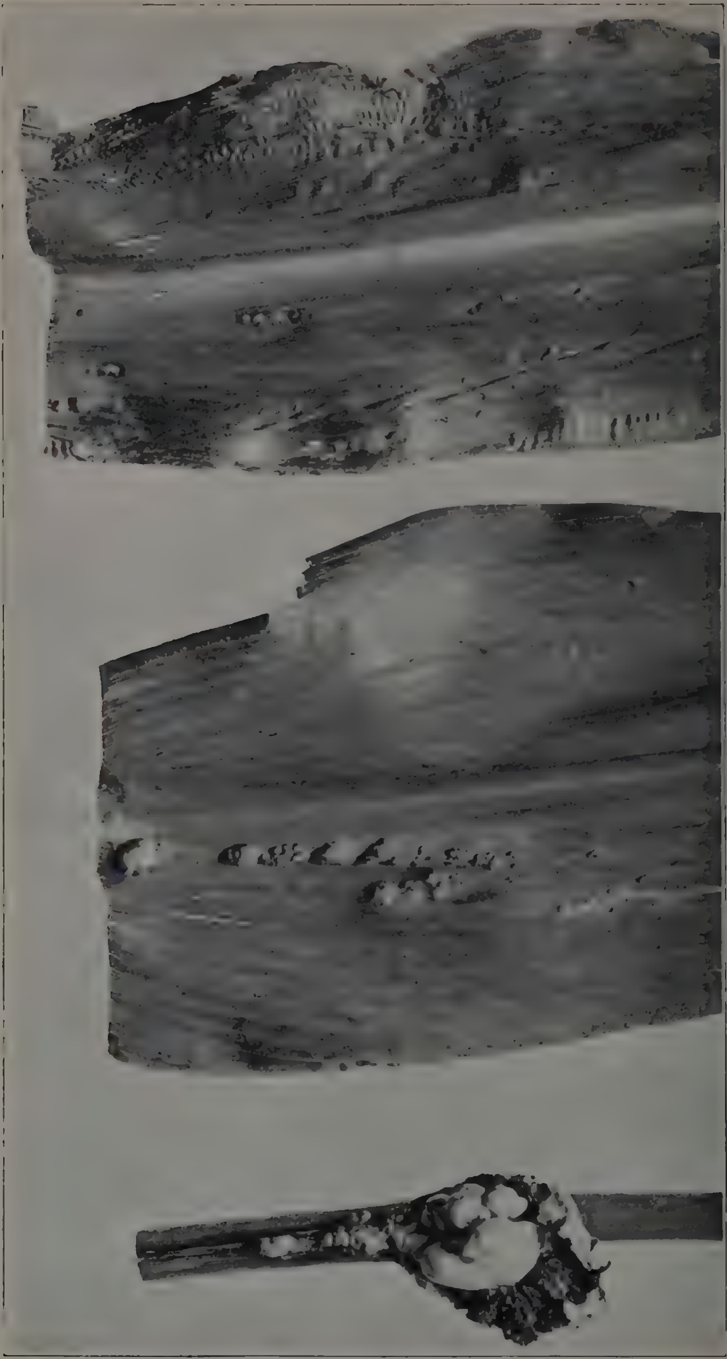

Fig. 1. "Incipient," "Warty," and "Small" Smut Boils

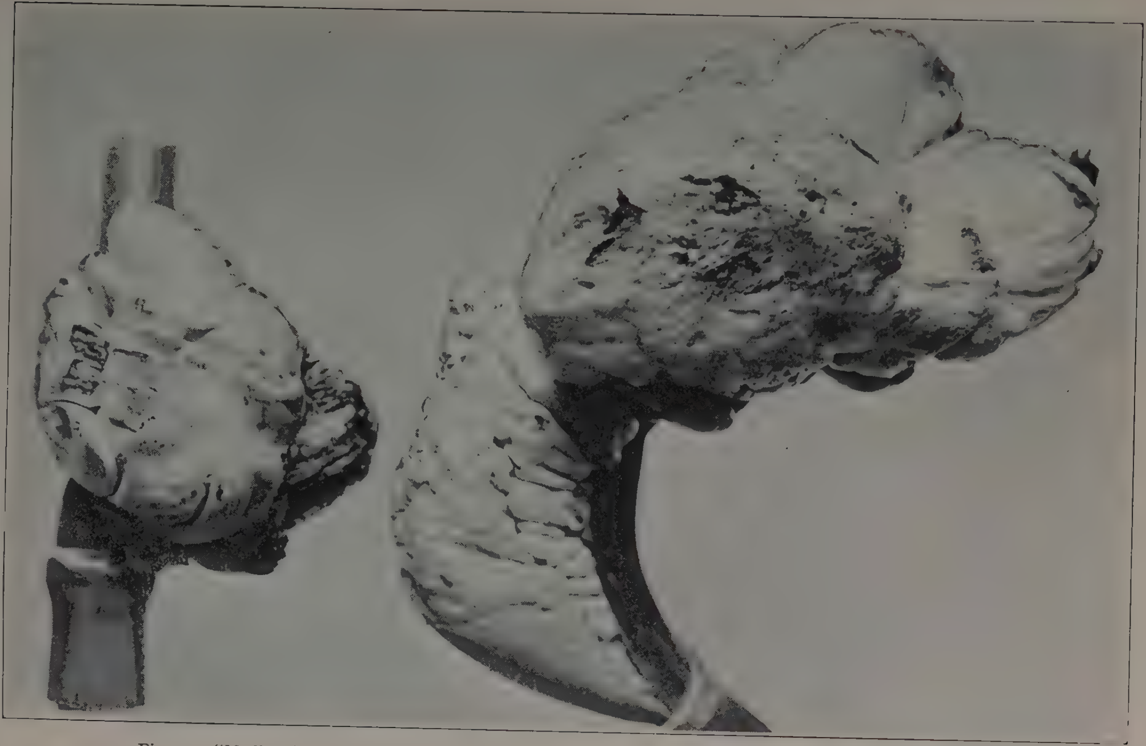

Fig. 2. "Medium" and "Large" Smut Boils, Used as a Basis in Classifying Size of Smut Boils

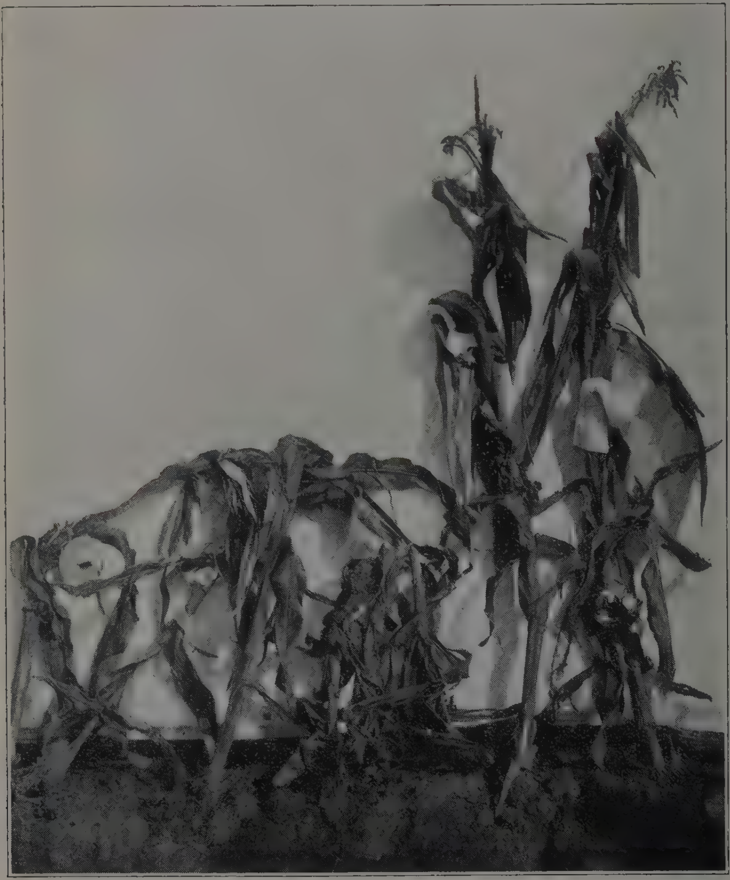

Fig. 3. Rustler High Smut Strain, Culture 28

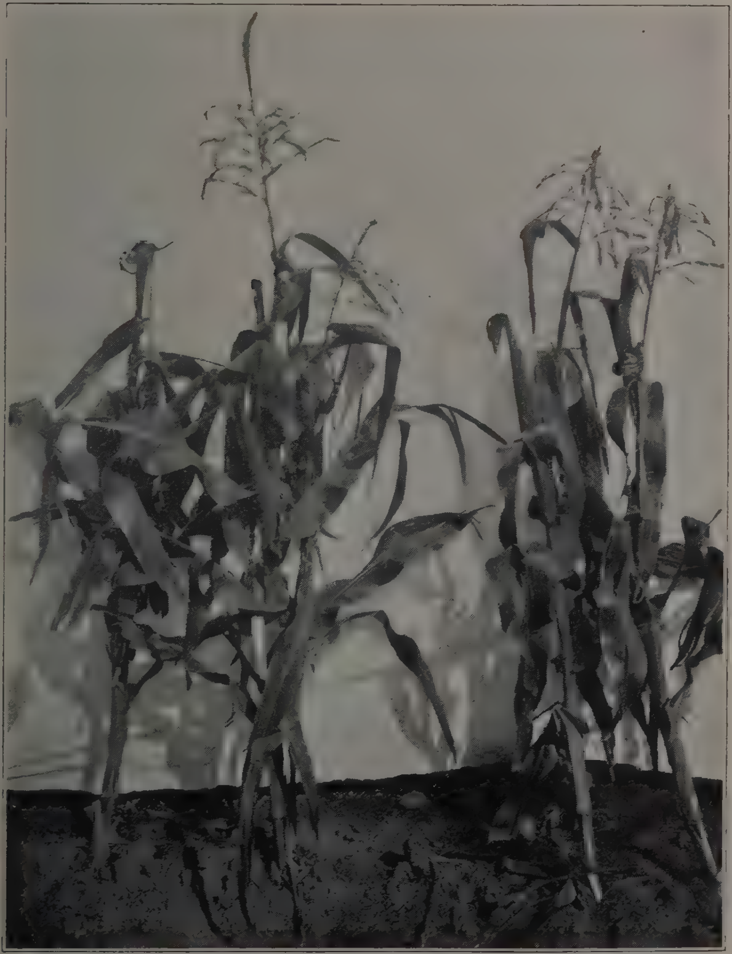

Fig. 4. Minnesota No. 13 Strain Showing Smut Boils on Necks of Plants as a Characteristic of this Strain

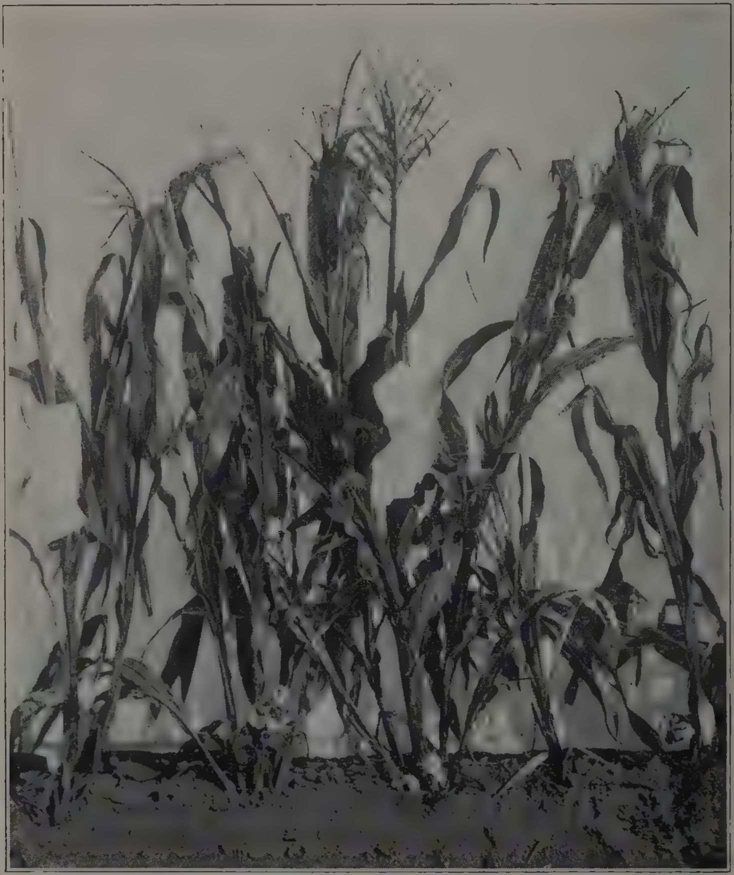

Fig. 5. Base and Lower Ear Bud Infections on a Yellow Endosperm Liguleless Strain, Culture 6

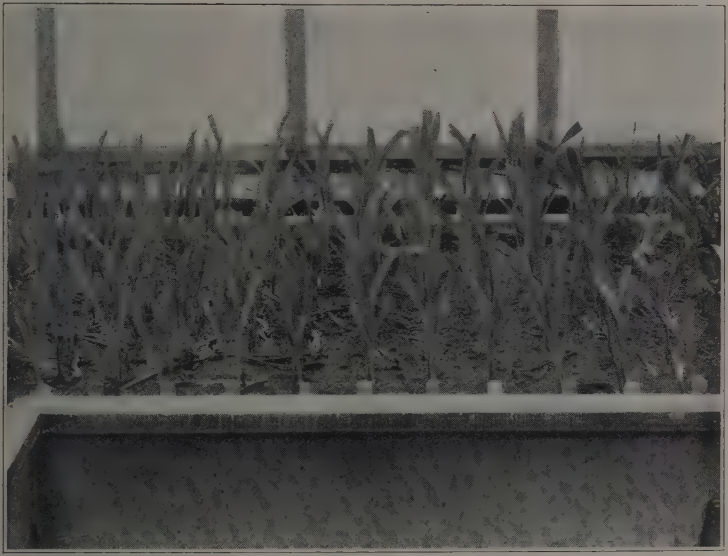

Fig. 6. Corn Seedlings Growing in Sand in the Greenhouse Bench on January 8, 1927, the Day They Were Inoculated, Hypodermically, with Smut Conidia

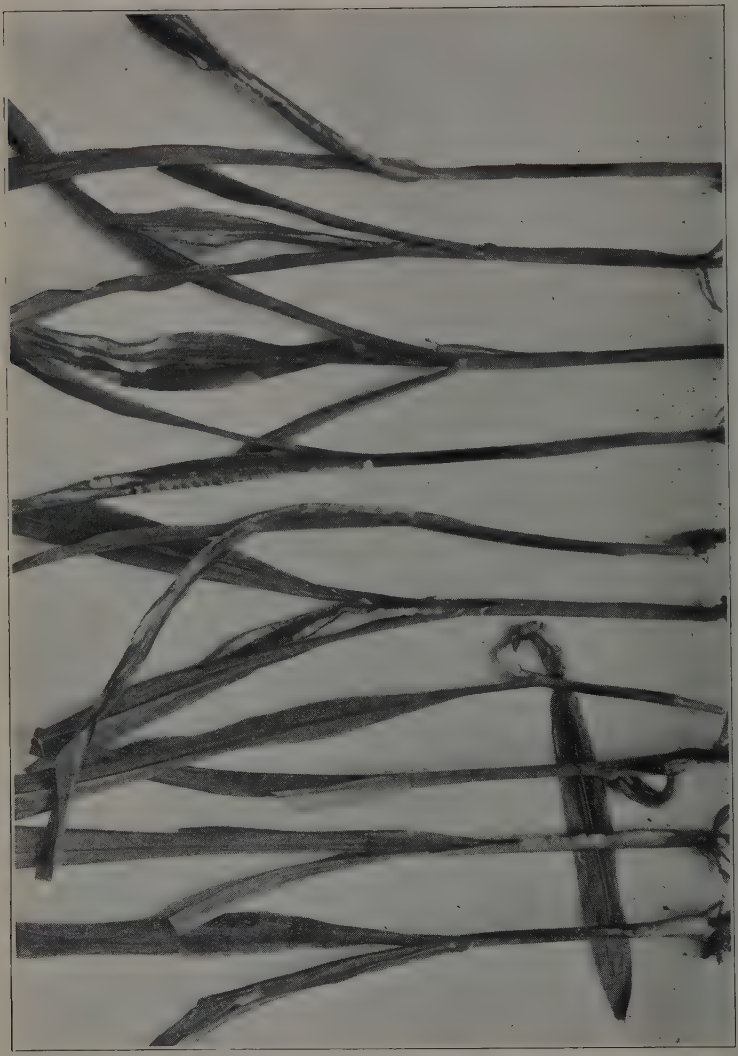

Fig. 7. Smut Infections on Corn Seedlings Inoculated in the Greenhouse with Smut Conidia, Showing Location and Degree of Smut Infections on Seedlings Photographed Jan. 21, 1927, the day smut infection notes were taken.

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CONTENTS

Page

The Minnesota bearing 6

Routine followed in tile tests 7

Test data and discussion 10

  Deflection of 30-inch tile under load 13

  Stresses in wall of 30-inch tile measured 14

  Modulus of elasticity of concrete in 30-inch tile 20

  Mathematical theory of stresses in pipe 20

  Mathematical solutions of stresses in circular pipe based on assumed pressure distributions 23

Deflection of beams 24

  Application to statically indeterminate structures 26

Mathematical analyses 27

  Analysis of sand bearing, uniform distribution of load 27

  Analysis of two-edge bearing 28

  Analysis of three-edge bearing 29

  Analysis of Minnesota bearing, uniform distribution of pressure 31

  Analysis of sand bearing, parabolic distribution of pressure 33

  Analysis of Minnesota bearing, parabolic distribution of pressure 34

  Stresses due to own weight, two-edge bearing 36

  Stresses due to own weight, sand and Minnesota bearings 37

  Deformation of vertical diameter, two-edge bearing 38

  Deformation of vertical diameter, sand bearing 39

  Deformation of vertical diameter, Minnesota bearing 40

Pressure distribution on circular pipe under load in sand bearings as measured by friction strips 41

Mathematical solutions of stresses in pipe under loadings measured by friction strips 51

Strength ratios of different bearings 59

Loads on pipes in trenches 61

Summary 63

Conclusions 64

Acknowledgments 65

Bibliography 65

ILLUSTRATIONS

Page

Fig. 1. Sand bearing 5
2. Two-edge bearing 5
3. Three-edge bearing 5
4. Minnesota bearing 6
5. Comparative tests of drain tile showing ratio between sand/three-edge and sand/Minnesota bearings 12
6. Ames dial used to measure deflection in 30-inch tile under load 13
7. Deformation of vertical diameter of 30-inch drain tile 14
8. Diagrammatic sketch of mirror compressometer, or strain gage 15
9. Points on 30-inch tile at which stresses were measured with tile under various loads 16
10. Stress-strain curves for prisms cut from 30-inch drain tile 20
11. Conditions of pressure distribution on circular pipe under load in the A.S.T.M. standard bearings for drain tile 22
12. Forces that hold a single quadrant of pipe in equilibrium 23
13. Short section of straight beam before and after flexure 24
14. Uniform distribution of load 27
15. Convention of signs 27
16. Two-edge bearing 28
17. Three-edge bearing 29
18. Minnesota bearing—uniform distribution of pressure 31
19. Sand bearing—parabolic distribution of pressure 33
20. Minnesota bearing—parabolic distribution of pressure 34
21. Stresses due to own weight—two-edge bearing 36
22. Stresses due to own weight—sand and Minnesota bearings 37
23. Deformation of vertical diameter—two-edge bearing 38
24. Steel strips in place as used in determining the pressure distribution in lower bearing of A.S.T.M. standard sand bearing 41
25. Position of steel strips for measuring distribution of pressure at top and bottom sand bearings 42
26. Effect of variation of moisture content of sand and compactness upon the distribution of pressure in the lower sand bearing 50
27. Effect of variation of moisture content of sand upon distribution of pressure in upper sand bearing 51
28. Actual loads on pipe—sand bearing 52
29. Values of coefficient K, as developed mathematically, for calculating moments for load distributions 60
30. Solution by nomograph of Marston formula for calculating loads on pipes in trenches 62

EXPERIMENTAL AND MATHEMATICAL ANALYSES OF DRAIN TILE TESTING AND NEW TEST BEARING[1]

By Dalton G. Miller[2] and Joseph A. Wise[3]

Three different bearings for strength tests of drain tile are recognized by the American Society for Testing Materials[4]: (1) the sand bearing (Fig. 1), in which the upper quadrant and the lower quadrant of the tile are imbedded in sand, through which the load is applied; (2) the two-edge bearing (Fig. 2), in which the load is applied at extremities of the vertical diameter, the upper and lower platens having plaster of paris contacts; and (3) the three-edge bearing (Fig. 3), in which the tile rests on two strips of wood one-half inch radius bevel on the inside while the load is applied through a plane bottom timber resting on the uppermost element of the tile.

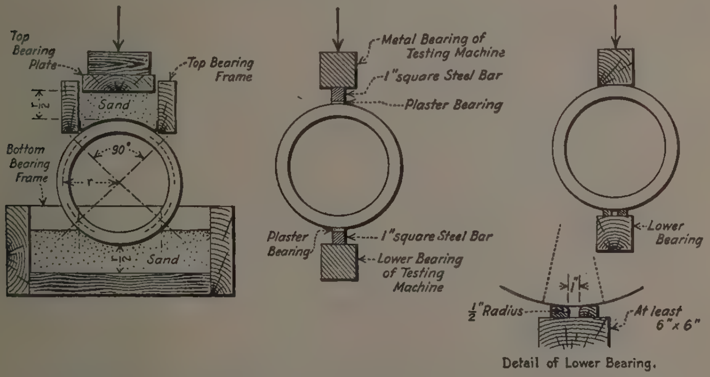

Fig. 1. Sand Bearing Fig. 2. Two-Edge Bearing Fig. 3. Three-Edge Bearing
Standard Bearings for Testing Drain Tile, 1927 Book of A.S.T.M. Standards

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[1] This paper is based on experiments at the drain tile laboratory, University Farm, St. Paul, Minn., conducted by the Department of Agriculture of the University of Minnesota, the Department of Drainage and Waters of the State of Minnesota, and the U. S. Department of Agriculture. These experiments were outlined primarily to simplify the testing, for strength, of drain tile of large diameter, altho the results of the work also apply to the testing of both sewer pipe and culvert pipe.

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[3] Assistant Professor of Structural Engineering, Civil Engineering Department, Univ. of Minn. (Formerly Junior Drainage Engineer, U. S. Dept. of Agr.)

[4] Standard Specifications for Drain Tile, 1927 Book of A.S.T.M. Standards.

In the course of the work in Minnesota several thousand drain tile, of sizes from 4 to 36 inches in diameter, have been tested, using for the most part the three-edge bearing, as this type is best suited for ordinary requirements, both in the laboratory and in the field, as it is generally necessary to keep the cost of testing at a minimum. Considerable difficulty, however, has been experienced with this bearing in the testing of tile as large in diameter as 22 inches and upward, owing to a tendency to roll out of the machine as the load is applied, unless the tile are truly circular in shape and of constant wall thickness. Also, tile that are out of shape or of non-uniform wall thickness will usually not have the center of gravity and geometrical center coincident. This introduces inaccuracies in the test.

The chief objection to the sand bearing is that it is tedious of application, particularly for tile of large diameter, while the same objection holds to a lesser degree for the two-edge bearing.

THE MINNESOTA BEARING

To obviate the difficulties with the three standard bearings, a new bearing, tentatively named the Minnesota (Fig. 4), is suggested. When the tests were outlined and until completed, it was thought that this bearing was entirely new. It later developed that this was not strictly true, as some years ago a few tile were tested at University Farm in which this bearing was used by John T. Stewart as a part of the earlier work of the A.S.T.M. committee on drain tile; also, rather peculiarly, the bearing was then called the "Minnesota" and was so referred to in reports covering the earlier work. For some reason no efforts were made after the first very meager tests to develop this bearing and so far as known no mathematical analysis of it has heretofore been offered, so that to all intents the Minnesota bearing, as considered in this paper, is new.

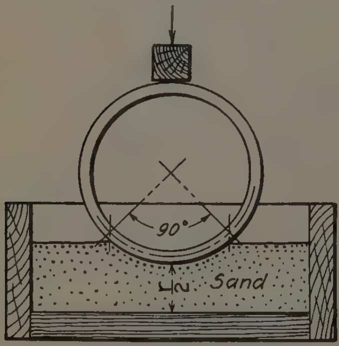


Fig. 4. Minnesota Bearing

As indicated in Figure 4, the lower quadrant of the tile, using the Minnesota bearing, is imbedded in sand as in the sand bearing, while the load is applied along the uppermost element of the tile through a timber, as in the three-edge bearing. This bearing has advantages over the sand bearing of simplicity and rapidity of application and eliminates the tendency of tile to roll, as with the three-edge bearing. In addition, tile that are out of shape or non-uniform in thickness will probably receive a more accurate test with this than with the three-edge bearing.

A series of tests was planned to determine experimentally the sand/Minnesota test ratio. It was decided to test tile at the same time on the three-edge bearing, because of its wide use, and to obtain further information as to the ratio between sand and three-edge bearing strengths.

A total of 1750 tile, from eight Minnesota tile plants, were tested, 378 of these being clay tile and 1372 concrete. Most of the tile tested were concrete, as they were more readily obtained. There is no reason to believe that the materials of which the tile were made had any appreciable effect on the strength ratios of the various bearings.

ROUTINE FOLLOWED IN TILE TESTS

A tile testing machine known as the Universal was used in this work. All tile up to 12 inches in diameter were broken directly upon the platform scales. The 14-inch tile 2 feet long, and the 16-inch tile 18 inches long were also tested directly. The longer 14- and 16-inch tile and all larger sizes were tested by means of a 1:5 ratio lever arm.

A minimum depth of sand equal to one-fourth of the internal diameter of the tile was maintained below the bottom of the tile and also above the top in the sand bearing. The upper sand box varied in size, depending upon the size of tile. It conformed as nearly as possible with the A.S.T.M. specifications. [1] Canvas was nailed to the box to retain the sand after the tile had collapsed. The smaller tile were tested in the three-edge bearing by means of a lower bearing placed upon the top of the sand box. A 4 x 6 inch oak block was placed below the lower bearing to increase rigidity and so cause a uniform distribution of load. The upper and lower bearing blocks were of oak and about 4 x 4 and 3 x 4 inches, respectively. A strip of white pine was used to face the upper bearing block of the three-edge and Minnesota bearings, while the two strips on the lower bearing of the three-edge bearing were of white pine. In order to eliminate accidental variations, as far as possible, the tile was tested in cyclic rotation: sand bearing, three-edge bearing, and Minnesota bearing. For the larger sizes, 20 inches and above, this was not done; instead, the order of testing was changed so that the sand and Minnesota bearings were used alternately and the three-edge bearing independently, the lower bearing being placed directly upon the lever arm. For most of the tests the sand was air dry, but for the 20-inch, 24-inch, and 30-inch tile it was lightly sprinkled.

All tile were taken from stock piles at the various plants and were at least three months old when tested. Many were a year or more old. In general, all tile appeared to have been well made, as the concrete tile were nominally of a 1-3 mix and the larger sizes contained considerable coarse aggregate (¼-¾ inch) while the clay tile were reasonably hard burned. The smaller concrete tile were made on rotating packer-head types of machines and the larger sizes were made on a tamping type or a more recently designed type of packer-shoe machine. The tile were carefully selected and only those of fairly uniform thickness and circular cross-sections were taken. Only tile without cracks, and otherwise sound, were taken, and the few that were cracked in shipping were not tested. A few in each group were tested for absorption in accordance with the A.S.T.M. standard test. [1]

The procedure at the laboratory was substantially as follows: The tile were stored upon arrival, some in the building and some outdoors. They were numbered and weighed and the diameter, length, and thickness of several tile of each size from every plant were measured. The tile were then distributed so that for each size from every plant the average weight was practically the same for all three bearings.

Most of the tile were tested as they came from the stock pile, without wetting, as it was thought that in making these bearing tests it made no appreciable difference whether the tile were wet, moist, or dry so long as the condition of all tile in any single series of tests was the same. However, in order to verify this assumption, 330 tile were selected and half were tested dry while the other half were tested after 14 hours immersion in a tank in the laboratory. As will be noted in Table I, the difference in the wet-dry ratio is very slight for the three types of bearings. Table I, altho not complete enough to establish an exact relation between the strength of tile tested wet and tile tested dry, does indicate quite definitely a lower strength for concrete tile tested wet. Whenever possible concrete tile should be tested wet, but if tested dry some allowance should be made for the fact that the results are unduly high.

There are not sufficient data at hand to establish any relationship between strength and absorption of clay tile tested wet and tested dry, but wet clay tile apparently do not lose as much in strength as do wet concrete tile. In any case the basis for all strength tests should be tile thoroly wet, preferably by immersion for at least 12 hours, and tests of dry tile should be made only when it is not expedient to test them wet.

TABLE I

Comparison of Results of Tile Tested Dry and Tile Tested Wet

Test bearing used	Internal diameter of tile	Av. absorption	Tile tested dry		Tile tested wet		Wet/dry ratio	Av. wet/dry ratio
			No. tested	Strength per lin. ft.	No. tested	Strength per lin. ft.		
				Concrete Tile				
	in.	per cent		lb.		lb.		
Sand	6	9.3	5	1956	5	1550	0.792	0.819
3-Edge	6		5	1276	5	1031	.808	
Minnesota	6		5	1256	5	1077	.857	
Sand	6	9.2	5	1828	5	1408	.770	.756
3-Edge	6		5	1207	5	913	.756	
Minnesota	6		5	1299	5	962	.741	
Sand	6	8.5	5	1368	5	1288	.942	.819
3-Edge	6		5	1041	5	745	.716	
Minnesota	6		5	1077	5	861	.799	
Sand	6	10.4	5	1570	5	1094	.697	.782
3-Edge	6		5	1012	5	791	.782	
Minnesota	6		5	954	5	826	.866	
3-Edge	6	11.1	10	981	9	909	.93	.93
Sand	8	11.4	5	1531	5	1265	.826	.827
3-Edge	8		5	1061	5	858	.809	
Minnesota	8		5	1057	5	893	.845	
Sand	8	8.5	4	1681	5	1418	.844	.875
3-Edge	8		4	1135	5	979	.863	
Minnesota	8		4	1055	5	967	.917	
3-Edge	8	8.2	5	1678	5	1177	.701	.701
Sand	10	10.6	5	1873	5	1315	.702	.690
3-Edge	10		5	1384	5	945	.683	
Minnesota	10		5	1467	5	1004	.684	
Sand	10	10.7	5	1663	5	1199	.721	.740
3-Edge	10		5	970	5	765	.789	
Minnesota	10		5	1130	5	803	.711	
Sand	10	10.6	5	1287	4	1120	.870	.829
3-Edge	10		5	905	5	739	.817	
Minnesota	10		5	938	5	749	.799	
3-Edge	10	8.7	4	1468	3	1221	.832	.832
Sand	12	9.2	5	2202	5	1982	.900	0.930
3-Edge	12		5	1470	5	1337	.910	
Minnesota	12		5	1493	5	1463	0.980	
3-Edge	12	9.8	5	1478	5	1543	1.044	1.044
3-Edge	15	7.6	4	1792	3	1489	0.831	0.831
3-Edge	28	5.3	5	3340	5	4005	1.199	1.199
3-Edge	28	9.4	3	1850	3	2133	1.153	1.153
3-Edge	30	11.4	5	1637	5	1588	0.970	0.970
				Clay Tile				
Sand	4	12.3	5	1947	5	2055	1.055	0.976
3-Edge	4		5	1492	5	1347	0.903	
Minnesota	4		5	1408	5	1366	.970	
Sand	8	12.9	5	1957	5	1949	.996	0.920
3-Edge	8		5	1463	5	1284	.878	
Minnesota	8		5	1418	5	1254	0.884	

TEST DATA AND DISCUSSION

Individual tile tests are not shown in this report, but the results have been summarized in Table II, while Figure 5, in which the abcissae are the internal diameter of the tile and ordinates the average strength ratios for each tile size, is based on Table II. The heavy horizontal lines in Figure 5 show the arithmetic average for each bearing, 4-inch tile being omitted in the average for the sand/three-edge ratio and sizes under 14 inches being omitted for the average of the sand/Minnesota ratio. The average for the sand/three-edge ratio for sizes 6 to 30 inches is 1.49, as determined experimentally, and for the sand/Minnesota ratio is 1.31 for sizes 14 to 30 inches. These results closely approximate ratios of 3/2 and 4/3 respectively. The results of the tests of the 4-inch tile were omitted in the average for the sand/three-edge ratio, as the load could not be applied properly to the 4-inch tile using the sand bearing because the tile pressed into the sand, sometimes as much as half its diameter. Sizes below 14-inch were omitted in the average of the sand/Minnesota ratio as the tests indicate an apparent tendency for this ratio to increase for tile of smaller diameter and, in any event, the practical application of the Minnesota bearing is for the larger tile.

TABLE II

Summarized Results of Tests of 1750 Drain Tile, 6 to 30 Inches in Diameter, Using Three Different Test Bearings

Diam. of tile	Manufacturer	Kind of tile	No. of tile	Breaking strength per lin. ft.			Strength ratios	
				Bearing				
				Sand	3-edge	Minn.	Sand 3-edge	Sand Minnesota
in.				lb.	lb.	lb.		
4	T	Clay	150	1960.4	1425.6	1400.6	1.375	1.400
6	T	Clay	138	2490.3	1557.0	1505.7	1.599	1.654
6	NN	Concrete	90	1704.5	1107.2	1138.9	1.539	1.497
6	A	Concrete	150	1514.7	1033.9	1058.7	1.465	1.431
6	S	Concrete	180	1902.2	1233.4	1260.2	1.542	1.509
6	B	Concrete	54	1410.7	922.5	940.6	1.529	1.500
Weighted average for 6-in.			612				1.534	1.520
8	S	Concrete	90	1536.7	1058.9	1107.6	1.451	1.387
8	NN	Concrete	30	1604.5	1030.2	1091.2	1.557	1.470
8	T	Clay	90	2026.1	1376.3	1366.9	1.472	1.482
8	B	Concrete	33	1506.1	1033.6	1004.9	1.457	1.499
8	A	Concrete	57	1538.5	1055.8	1070.1	1.457	1.438
Weighted average for 8-in.			300				1.470	1.446
10	S	Concrete	90	1823.9	1280.7	1330.1	1.424	1.371
10	NN	Concrete	30	1431.0	868.0	967.0	1.649	1.480
10	B	Concrete	30	1212.4	822.2	843.6	1.475	1.437
10	A	Concrete	30	1780.4	1222.6	1249.9	1.456	1.424
Weighted average for 10-in. ...			180				1.475	1.409

TABLE II—*Continued*

Diam. of tile	Manu-facturer	Kind of tile	No. of tile	Breaking strength per lin. ft.			Strength ratios	
				Bearing			Sand 3-edge	Sand Minnesota
in.				Sand lb.	3-edge lb.	Minn. lb.		
12	NN	Concrete	30	2023.1	1331.3	1374.8	1.520	1.472
12	A	Concrete	30	2092.0	1403.5	1476.3	1.491	1.417
12	S	Concrete	87	1762.6	1199.2	1277.2	1.470	1.380
Weighted average for 12-in. ...			147				1.484	1.406
14	F	Concrete	30	1838.0	1232.4	1423.0	1.491	1.292
14	S	Concrete	25	2449.6	1603.5	1754.9	1.528	1.396
Weighted average for 14-in. ...			55				1.508	1.339
16	F	Concrete	30	2133.0	1538.2	1727.8	1.387	1.235
16	S	Concrete	30	2203.4	1495.1	1637.0	1.474	1.346
16	B	Concrete	27	2458.0	1596.7	1702.0	1.539	1.444
Weighted average for 16-in. ...			87				1.464	1.338
20	B	Concrete	24	2311.5	1735.8	1954.8	1.332	1.182
20	F	Concrete	24	2373.0	1529.3	1836.8	1.552	1.292
20	S	Concrete	21	1673.3	1347.7	1412.9	1.242	1.184
20	X	Concrete	30	1872.5	1457.0	1572.5	1.285	1.191
20	II	Concrete	24	1916.0	1461.3	1558.0	1.311	1.230
Weighted average for 20-in. ...			123				1.344	1.215
24	F	Concrete	15	2361.6	1523.2	1714.4	1.550	1.378
24	S	Concrete	15	3341.8	2118.4	2572.4	1.578	1.299
24	B	Concrete	15	3396.8	2014.0	2475.2	1.687	1.372
26	X	Concrete	9	2871.3	2101.3	2456.0	1.366	1.169
Weighted average for 24- and 26-in.			54				1.565	1.320
30	F	Concrete	15	5191.2	3706.0	4194.4	1.401	1.238
30	B	Concrete	15	5098.8	3208.8	3609.2	1.589	1.413
30	S	Concrete	12	6260.5	3713.5	4703.5	1.686	1.331
Weighted average for 30-in. ...			42				1.550	1.327
Arithmetic average of weighted averages for each size, 6 to 30 in.........							1.488	
Arithmetic average of weighted averages for each size, 14 to 30 in........								1.307

The average variation from the mean of the tests made in each bearing was computed on the basis of weighted averages for each size and plant. The results are recorded in Table III.

These experimental data indicate that all three bearings are about equally reliable, as any difference is too slight to be of consequence. However, for the large tile the difference in favor of the Minnesota bearing was somewhat greater than for the average.

After completing the tests of the 1750 tile, as recorded in Table II and plotted in Figure 5, it was decided to follow up this work along somewhat different lines in order better to analyze the actual relation of tests of drain tile made in the three bearings and, if possible, to present exact mathematical solutions for each type of bearing, thereby fixing exact reduction ratios. This is the purpose of the following experiments and discussion.

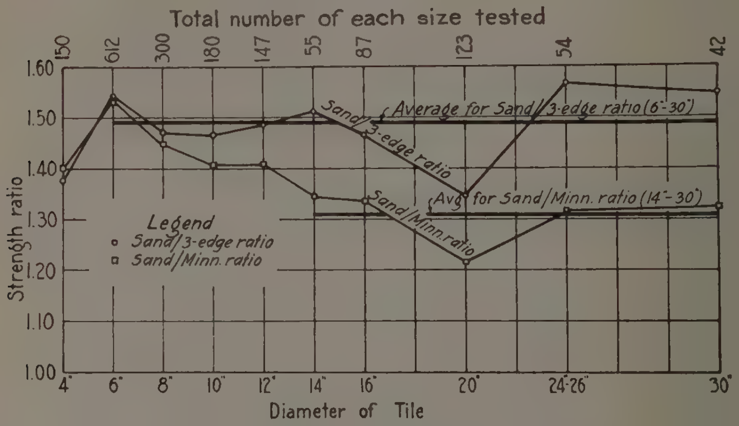


Fig. 5. Comparative Tests of Drain Tile Showing Ratio Between Sand/Three-Edge and Sand/Minnesota Bearings

TABLE III

Average Variation in per Cent from the Mean of Tile Tested in Different Bearings

Diameter of tile	Sand bearing		3-edge bearing		Minnesota bearing	
	No. tested	Weighted average	No. tested	Weighted average	No. tested	Weighted average
			Concrete Tile			
in.		per cent		per cent		per cent
6	158	9.47	158	8.95	158	8.96
8	70	9.34	70	8.95	70	6.65
10	60	9.82	60	11.13	60	10.76
12	49	7.34	49	8.24	49	7.53
14	18	8.70	18	6.04	19	12.29
16	29	7.98	29	8.29	29	7.40
20	41	8.27	41	5.96	41	6.99
24 & 26	18	7.83	18	6.87	18	5.60
30	14	8.18	14	5.49	14	4.32
Totals	457	...	457	...	458	...
Mean weighted av.	...	8.94	...	8.52	...	8.28
Arithmetic av.	...	8.55	...	7.75	...	7.72
			Clay Tile			
4	50	10.64	50	10.70	50	11.79
6	46	9.45	46	11.77	46	12.45
8	30	7.09	30	12.05	30	7.67
Totals	126	...	126	...	126	...
Mean weighted av.	...	9.36	...	11.41	...	11.05
Arithmetic av.	...	9.06	...	11.51	...	10.64
			Summary			
Grand total	583	...	583	...	584	...
Combined weighted averages	...	9.03	...	9.14	...	8.88
Combined arithmetic averages	...	8.68	...	8.69	...	8.53

Deflection of 30-Inch Tile Under Load

One of the 30-inch concrete tile was loaded under each of the three bearings and the deformation of its vertical diameter was measured, using three Ames dials reading to 0.001 inch, one being placed at each end and one in the center of the tile. They were lightly wedged in place as shown in Figure 6. This tile was of high quality, made on a tamping type machine. It was not corrugated on the exterior, but was slightly barrel shape, because it had been manufactured from a very plastic mix. The tile was nominally 30 inches long with wall thickness of 3 inches. Its actual average diameter was 30 inches, its length 29 inches, and its wall thickness 3.2 inches.

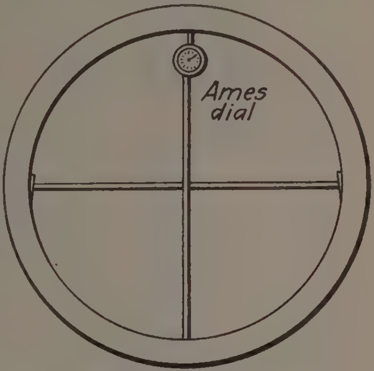


Fig. 6. Ames Dial Used to Measure Deflection in 30-Inch Tile Under Load

Figure 7 shows the actual deformation, as determined experimentally, of the vertical diameter of this tile under loads of 1500, 3000, and 5000 pounds applied through each of the three bearings. The deformation (δ) also has been calculated for the three bearings by equations 31, 32, and 33, using the value of 6,360,000 pounds per square inch as the modulus of elasticity of the concrete.

In Table IV are compared the actual and theoretical deflections of the tile in the three bearings under the 5000-pound load.

TABLE IV

Comparison of Actual and Theoretical Deflections of 30-Inch Tile 29 Inches Long Under 5000-Pound Load in Different Bearings

	Three-edge bearing	Minnesota bearing	Sand bearing
	in.	in.	in.
Actual deflection	0.0084	0.0078	0.0074
Theoretical deflection	0.0072	0.0065	0.0059

A study of Table IV shows that the experimental deflection for each bearing when compared with the theoretical deflection gives results between 17 and 25 per cent more. This is satisfactory agreement, and several factors might easily account for differences as small as these and will not be discussed.

Using the deflection values of Table IV and calculating the three-edge/sand, three-edge/Minnesota, and the Minnesota/sand ratios, as determined experimentally, the results are 1.14, 1.08, and 1.05; while the ratios as derived theoretically are respectively 1.22, 1.11, and 1.10.

The theoretical values agree with the experimental as well as could be reasonably expected.

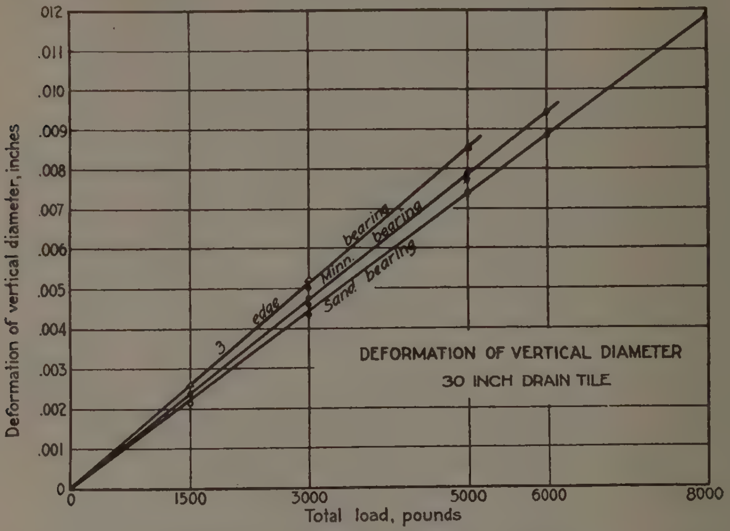


Fig. 7. Deformation of Vertical Diameter of 30-Inch Drain Tile

Stresses in Wall of 30-Inch Tile Measured

Stresses in the wall of the same 30-inch concrete tile that was used in the deflection tests were measured by a strain gauge with the tile under different loads and in the various bearings. As the unit stresses were very low, being limited by the tension in the concrete, it was necessary to use a special instrument and an adaptation of the Martens [2] compressometer was devised, as shown in Figure 8.

A and B are pieces of heavy brass fastened to the specimen by two screws C and D. The distance between C and D forms the gage line length G, about 2 inches in these tests. P is a very short (0.2 inch) hard steel pin sharpened to a true point at each end. The rod R is attached to the pin and carries a polished stellite mirror, M. A short pin attached to B supports R and prevents it from dropping. The pin P fits into punch marks in B and A. F carries a fixed mirror that is used as standard. Any change ΔG in the gage length G will rotate the mirror M, and for small angles the angle of rotation will be $\frac{\Delta G}{W}$. If a scale S is placed a distance L from the mirror and its reflection in the mirror is viewed through a transit, T, the crosshair of the transit will appear to move a distance, S, along the scale. The angle of rotation of the mirror will be $\frac{S}{2L}$. Therefore $\frac{\Delta G}{W}=\frac{S}{2L}$ or $\Delta G=\frac{SW}{2L}$ (Equation 1). The unit deformation will be $\frac{\Delta G}{G}=\frac{SW}{2LG}$ (Equation 2). In the tests described W was 0.2 inch, L was about 300 inches, G was 2 inches, and the least reading of the scale was 0.01 inch, so that the least deformation that could be read was $\frac{.01 \times .2}{2 \times 300 \times 2}=.0000017$ inch or about two millionths of an inch. Corresponding to a modulus of elasticity of 6,000,000, the unit stresses were measured to about 10 pounds per square inch. Strain gage measurements, as recorded in Table V, were taken at the inner and outer surfaces of the tile, as indicated in Figure 9.

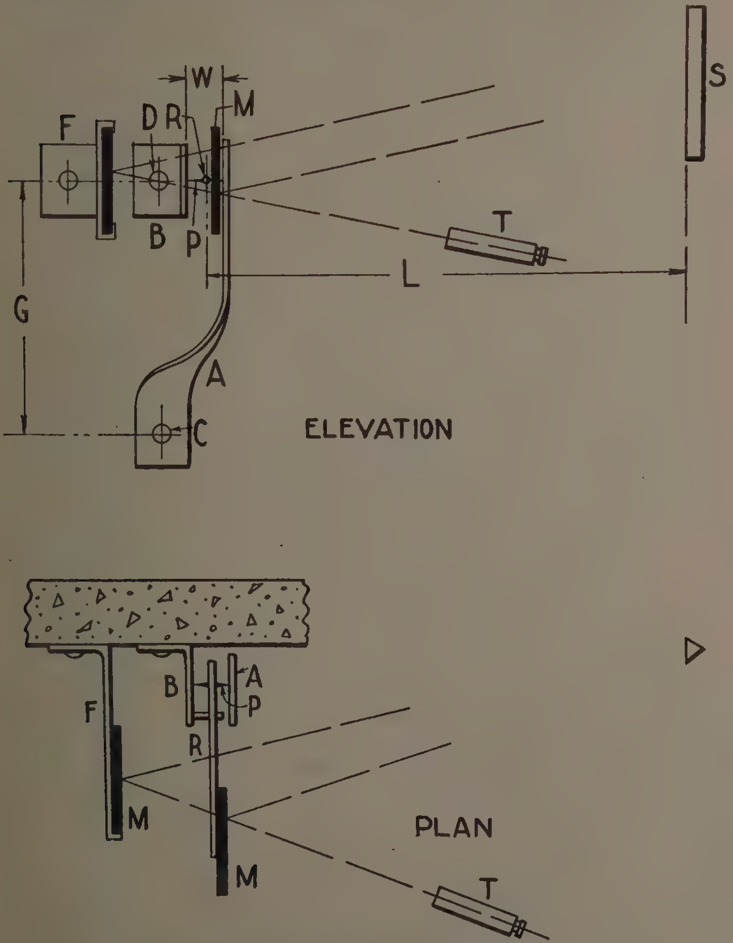


Fig. 8. Diagrammatic Sketch of Mirror Compressometer, or Strain Gage

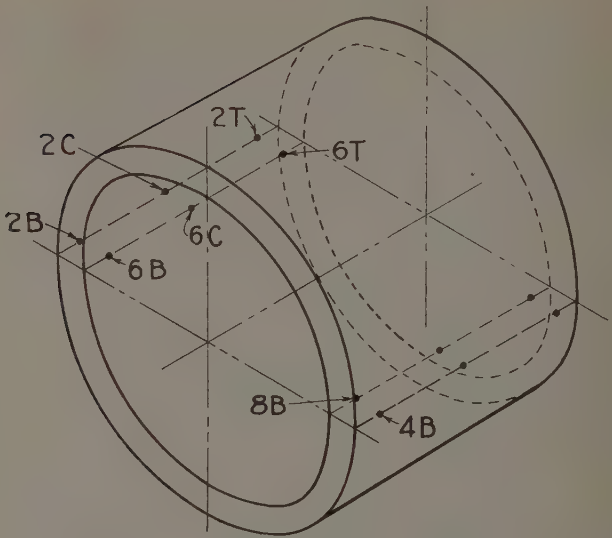


Fig. 9. Points on 30-Inch Tile at Which Stresses Were Measured with Tile Under Various Loads

TABLE V

STRAIN-GAGE MEASUREMENTS OF STRESSES AT DIFFERENT POINTS IN THE WALLS OF A DRAIN TILE 30 INCHES IN DIAMETER AND 29 INCHES IN LENGTH WHEN UNDER VARIOUS LOADS IN THREE DIFFERENT TEST BEARINGS

Total load on tile	Readings on engineer's scale (50 divisions to inch)						δ_u Unit deformation	f Fiber stress in pipe per sq. in.
	1	2	3	Av. of 1-3	Calculated readings	Reduced to inches		
	SAND BEARING							
	Gage on pipe at 4-B. G=2.00 in. L=290.4 in.							
lb.						in.	in.	lb.
500	Average of four sets of readings			0	1.7	-0.034	0.0000059	30
1500				3.3	5.0	.100	.0000172	88
3000				8.2	10.1	.202	.0000348	177
5000				15.0	16.8	.336	.0000579	295
6000				18.5	20.2	.404	.0000696	354
	Gage on pipe at 2-B. G=1.93 in. L=295.2 in.							
500	0	0		0	1.8	.036	.0000063	32
1500	3.7	2.7		3.2	5.4	.108	.0000190	97
3000	10.2	7.7		9.0	10.8	.216	.0000379	193
5000	17.7	14.7		16.2	18.0	.360	.0000632	322
6000	21.9	17.7		19.8	21.6	.432	.0000758	386
	Gage on pipe at 2-C. G=1.98 in. L=307.2 in.							
500	Average of five sets of readings			0	1.2	.024	.0000039	20
1500				1.5	3.5	.070	.0000115	59
3000				4.8	7.0	.140	.0000230	117
5000				8.4	11.7	.234	.0000385	196
6000				10.6	14.1	.282	.0000464	236
8000				17.6	18.8	.376	.0000618	314

TABLE V—*Continued*

Total load on tile lb.	Readings on engineer's scale (50 divisions to inch) 1	2	3	Av. of 1-3	Calculated readings	Reduced to inches in.	δu Unit deformation in.	f Fiber stress in pipe per sq. in. lb.
Gage on pipe at 2-T. G=2.00 in. L=312.6 in.								
500	0	0		0	1.6	.032	.0000051	26
1500	2.5	2.8		2.7	4.9	.098	.0000157	80
3000	8.0	7.8		7.9	9.8	.196	.0000313	159
5000	15.2	14.0		14.6	16.4	.328	.0000525	267
6000	18.9	17.0		18.0	19.6	.392	.0000627	319
Gage on pipe at 8-B. G=1.96 in. L=290.4 in.								
500	Average of three sets of readings			0	2.4	.048	.0000084	43
1500				4.0	7.1	.142	.0000249	127
3000				11.4	14.2	.284	.0000499	254
5000				20.5	23.7	.474	.0000833	424
6000				26.1	28.5	.570	.0001001	509
Gage on pipe at 6-B. G=2.05 in. L=289.4 in.								
500	0	0		0	3.2	.064	.0000108	55
1500	7.2	7.0		7.1	9.7	.194	.0000327	166
3000	18.0	15.5		16.7	19.3	.386	.0000651	331
5000	33.3	27.5		30.4	32.2	.644	.0001086	553
6000	37.8	33.0		35.4	38.6	.772	.0001301	662
Gage on pipe at 6-C. G=2.09 in. L=300.6 in.								
500	0	0		0	2.1	.042	.0000067	34
1500	3.7	4.2		4.0	6.4	.128	.0000204	104
3000	11.2	10.9		11.1	12.8	.256	.0000407	207
5000	20.0	19.0		19.5	21.3	.426	.0000678	345
6000	24.7	22.0		23.4	25.5	.510	.0000812	413
Gage on pipe at 6-T. G=2.05 in. L=312.6 in.								
500	0	0		0	2.7	.054	.0000084	43
1500	5.0	5.5		5.3	8.1	.162	.0000253	129
3000	13.2	13.7		13.5	16.1	.322	.0000502	255
5000	24.7	24.0		24.4	26.9	.538	.0000840	427
6000	29.7	29.5		29.6	32.3	.646	.0001008	513
THREE-EDGE BEARING Gage on pipe at 2-C. G=1.98 in. L=300.6 in.								
500	0	0	0	0	1.8	.036	.0000060	31
1500	3.7	3.0	4.0	3.6	5.5	.110	.0000185	94
3000	9.7	8.0	9.0	8.9	10.9	.218	.0000366	186
5000	17.2	16.0	16.0	16.4	18.2	.364	.0000612	311
Gage on pipe at 2-T. G=2.00 in. L=312.6 in.								
500	0	0		0	2.0	.040	.0000064	33
1500	3.7	5.0		4.4	5.9	.118	.0000189	96
3000	8.7	10.0		9.3	11.9	.238	.0000381	194
5000	16.7	19.0		17.8	19.8	.396	.0000633	322
Gage on pipe at 6-C. G=2.09 in. L=300.6 in.								
500	0	0	0	0	3.0	.060	.0000096	49
1500	5.7	6.0	6.5	6.1	9.0	.180	.0000287	146
3000	18.7	15.0	16.0	16.6	18.1	.362	.0000576	293
5000	27.2	27.0	27.0	27.1	30.1	.602	.0000958	487
Gage on pipe at 6-T. G=2.05 in. L=312.6 in.								
500	0	0		0	3.1	.062	.0000097	49
1500	6.0	6.2		6.1	9.2	.184	.0000287	145
3000	14.2	15.7		15.0	18.3	.366	.0000571	291
5000	26.4	28.5		27.5	30.6	.612	.0000955	486

TABLE V—*Continued*

Total load on tile lb.	Readings on engineer's scale (50 divisions to inch)						δ_u Unit deformation in.	f Fiber stress in pipe per sq. in. lb.
	1	2	3	Av. of 1-3	Calculated readings	Reduced to inches in.		
MINNESOTA BEARING Gage on pipe at 2-C. G=1.98 in. L=307.2 in.								
500	0	0	0	0	1.5	.030	.0000049	25
1500	4.0	3.7	2.7	3.5	4.4	.088	.0000145	74
3000	8.3	8.5	7.2	8.0	8.7	.174	.0000286	146
5000	13.3	14.5	13.2	13.7	14.5	.290	.0000477	243
6000	16.0		15.9	16.0	17.5	.350	.0000575	293
Gage on pipe at 2-T. G=2.00 in. L=312.6 in.								
500	0	0		0	2.1	.042	.0000067	34
1500	3.7	3.3		3.5	6.2	.124	.0000198	101
3000	9.4	9.5		9.5	12.4	.248	.0000397	202
5000	19.4	17.7		18.6	20.5	.410	.0000656	334
6000	23.4	21.7		22.6	24.6	.492	.0000787	400
Gage on pipe at 6-T. G=2.05 in. L=312.6 in.								
500	0	0		0	2.9	.058	.0000091	46
1500	5.5	6.0		5.8	8.8	.176	.0000275	140
3000	14.0	14.8		14.4	17.7	.354	.0000552	281
5000	26.2	26.8		26.5	29.5	.590	.0000921	468
6000	32.4	32.2		32.4	35.3	0.706	0.0001102	561

δ = deformation of concrete in gage length
G = gage length, in.
W = width of moving pin=0.20 in.
E = modulus of elasticity (initial) = 6,360,000 lb. per sq. in.

δ_u = unit deformation of concrete.
L = distance from mirror to scale, in.
S = reading of scale, in.
f = fiber stress in concrete.

Formulae

$$\delta_u = \frac{SW}{2GL} \text{ (Eq. 2)} \qquad f = .8E\,\delta_u \text{ (Eq. 3) (factor .8 is due to instrument)}$$

From the data of Table V, the actual fiber stresses were determined by Equations (3) and (2) for the different points as recorded in Table VI. The factor 0.8 used in Equation (3) is an instrument constant due to the fact that the deformation of the concrete was not measured, by the device used, at the exact surface of the tile but 0.4 inch from it.

The calculated scale reading for any load, in Table V, is $\left(\frac{\text{load}}{\text{maximum load} - 500}\right)$ multiplied by the maximum scale reading recorded in the column headed "Av. of 1-3."

Theoretical fiber stresses where strain gage measurements were taken, when calculated by the modulus of rupture formula $f=\frac{6M}{t^2}$ (Equation 4) in which t is the thickness of the tile wall, in inches, and M is the bending moment in the wall of the tile expressed in pound-inches per inch of length (as calculated from equations and developed in this bulletin) are shown in Table VII and compared with the fiber stresses as determined by Equation (3) as shown in Table VI.

TABLE VI

FIBER STRESSES IN WALLS OF 30-INCH PIPE WHEN UNDER A TOTAL LOAD OF 5000 POUNDS IN THREE DIFFERENT TEST BEARINGS

Data Summarized from Table V

Location of gage on pipe (See Fig. 9)	Fiber stresses at 5000-lb. load	
	Compression	Tension
	SAND BEARING	
4-B		295
2-B		322
2-C		196
2-T		267
Average		270
8-B	424	
6-B	553	
6-C	345	
6-T	427	
Average	437	
	THREE-EDGE BEARING	
2C		311
2-T		322
Average		316
6-C	487	
6-T	486	
Average	486	
	MINNESOTA BEARING	
2-C		243
2-T		334
Average		288
6-T	468	

TABLE VII

BENDING MOMENT AND MODULUS OF RUPTURE CALCULATED FOR SAND, MINNESOTA, AND THREE-EDGE BEARINGS

			From Table VI
Sand bearing, uniform loading	$M = .1545\ Pr. = 442$	$f = 258$ (13)	270
Sand bearing, parabolic loading	$M = .1655\ Pr. = 473$	$f = 277$ (19)	270
Minnesota bearing, uniform loading	$M = .1682\ Pr. = 481$	$f = 283$ (18a)	288
Minnesota bearing, parabolic loading	$M = .1737\ Pr. = 480$	$f = 280$ (24)	288
Two-edge bearing	$M = .1817\ Pr. = 519$	$f = 304$ (15)	316

$P = \frac{5000}{29} = 172.4$ (load in lb. per in. of length)

$r = 16.6$ in., radius of tile to center line of wall

$t = 3.2$ in., thickness of tile wall

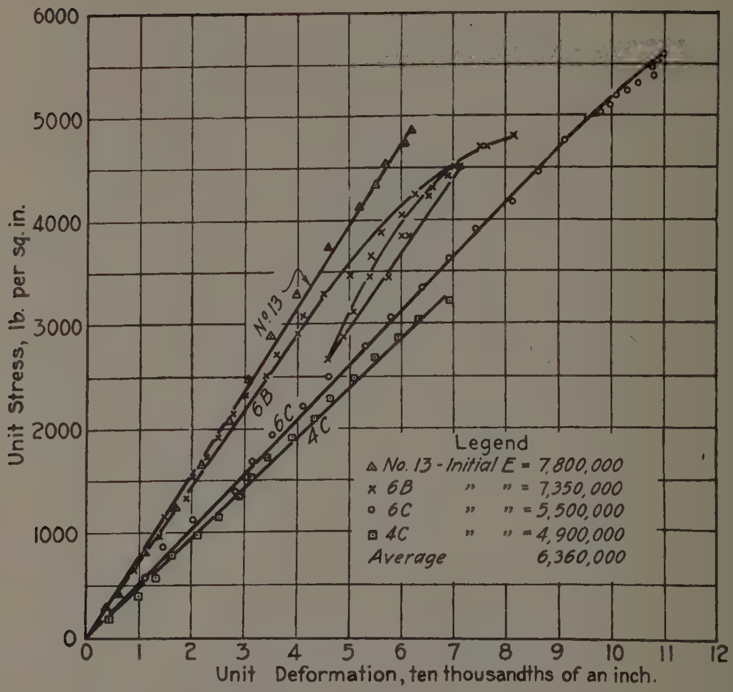


Fig. 10. Stress-Strain Curves for Prisms Cut from 30-Inch Drain Tile

Modulus of Elasticity of Concrete in 30-Inch Tile

After completing the deflection and stress tests, the 30-inch tile was tested to destruction, and prisms roughly 3 x 3 x 6 inches were cut from the wall. These were tested in compression in a 100,000 pound Olsen testing machine and the stress-strain curve of the prisms was developed as shown in Figure 10. By this work the modulus of elasticity (E) was found to be 6,360,000 and this is the value used in the calculations.

Mathematical Theory of Stresses in Pipe

The problem of the elastic circular pipe is a special case of the problem of curved beams and, it is believed, was first analyzed by Dr. E. Winkler in 1858 [3]. In this early memoir the circular ring subjected to oppositely directed loads at the extremities of a diameter, is considered and its analysis is applied to chain links. The analysis also appeared in 1867 in the same author's book "Elasticitatslehre" [4]. Todhunter and Pearson [5] summarized Dr. Winkler's work in 1886 and apparently gave him credit for priority in the solution of the circular ring. So far as known, the first analysis applied to pipe of the type of drain tile and culvert pipe was by E. J. Fort and C. W. L.

Filkins in 1895 [6]. These men considered the cases of opposed diametral loading and of uniform loads distributed over the full width of pipe. Fort and Filkins gave credit to J. Resal [7] and A. Madamet [8] for having solved the problem of the elastic ring with opposed diametral loads. In 1908 A. N. Talbot [9] cited analyses from the thesis of W. Slater in which the opposed diametral loading and types of uniformerly distributed loadings were investigated analytically. Modifications of the results for thick rings were also given. Finally, in 1913, the analyses for uniform loading distributed over various portions of the width were given by A. Marston and A. O. Anderson [10]. A more exact and rigorous solution for circular rings was indicated in 1924 by Dr. A. Föppl and Dr. L. Föppl [11].

For circular pipe tested in either sand or Minnesota bearings, the distribution of pressure is not uniform. When the tile referred to in this bulletin were tested, during the summer of 1924, no exact information was available as to the distribution of this pressure, and mathematical solutions of the sand and the Minnesota bearings were therefore attempted on the assumptions that the distribution was (1) uniform and (2) after trial, parabolic. From these two assumptions, equations (14), (18), (20), and (21) were developed. Solving these equations, however, did not give results that closely checked the experimental data. As it was thought that the general principles of the mathematical analyses were correct and that enough tile had been tested to establish fairly well the accuracy of the experimental data, the indications seemed to be that the trouble was in the assumptions made as to pressure distribution. The method of measuring this pressure distribution by friction strips, as later described, was therefore developed, following which, mathematical solutions were made that it is believed more accurately represent true conditions than do these first solutions.

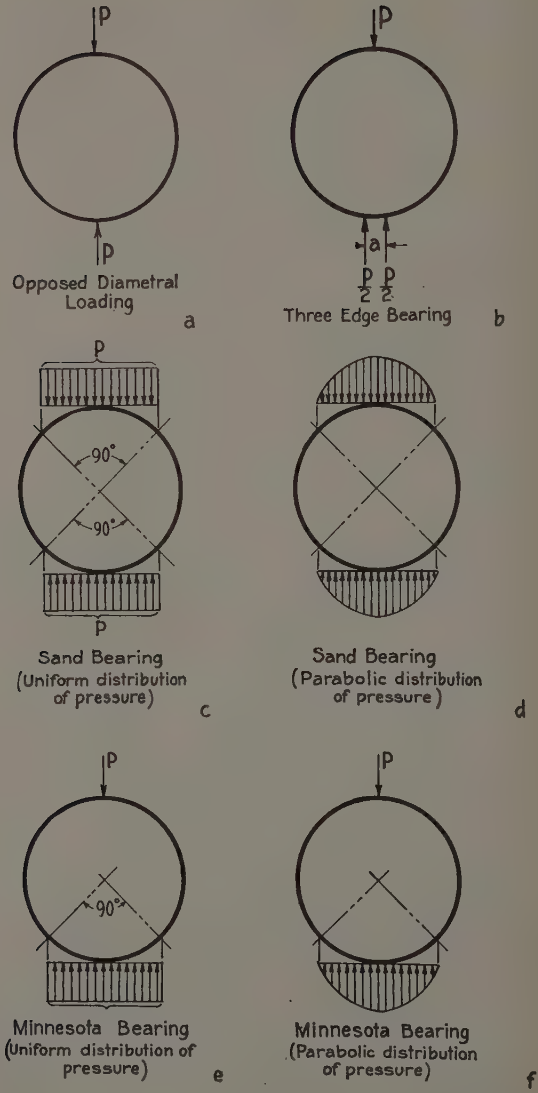

P
P
Opposed Diametral Loading
a
P
a
P/2 P/2
Three Edge Bearing
b
P
90°
90°
P
Sand Bearing (Uniform distribution of pressure)
c
Sand Bearing (Parabolic distribution of pressure)
d
P
90°
Minnesota Bearing (Uniform distribution of pressure)
e
P
Minnesota Bearing (Parabolic distribution of pressure)
f

Fig. 11. Conditions of Pressure Distribution on Circular Pipe Under Load in the A.S.T.M. Standard Bearings for Drain Tile as Assumed Previous to Measuring the Distribution by Friction Strips

Mathematical Solutions of Stresses in Circular Pipe Based on Assumed Pressure Distributions

The different types of analyses are illustrated in Figure 11. They are approximations to the three types of bearing shown in Figures 1, 3, and 4. In order to explain the method of analysis, assume the conditions of loading illustrated in Figure 11(a); the case of opposed diametral loading. If we consider a vertical and a horizontal axis through the center of a pipe, we see immediately that both are axes of symmetry. We can then deal with a single quadrant, as shown in Figure 12.

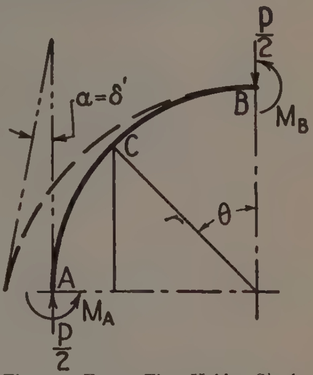


Fig. 12. Forces That Hold a Single Quadrant of Pipe in Equilibrium

This quadrant will be held in equilibrium by the forces there shown. There will be no shear at either A or B because if those places were cut there would be no tendency for the adjacent surface to move laterally with reference to A or B. This is evident from the symmetry of the figure. Also, there can be no axial stress at B as there is no other horizontal force acting. We have then a vertical force $\frac{P}{2}$ at B, an axial force $\frac{P}{2}$ at A, and moments M_A and M_B at A and B. Call the radius of the pipe r and measure angles from the vertical. If we consider moment M_A removed, owing to the action of force $\frac{P}{2}$ the pipe will bend as shown by the dotted lines and the tangent at A will now be rotated from its original position by an angle $\propto = \delta'$. If we have a unit moment acting at A, it will produce a deflection which we will call δ_1. We know, however, from symmetry that the tangent at A remains vertical and so the moment M_A must be equal to $\frac{\delta'}{\delta_1}$. This type of analysis holds good for any loading that produces biaxial symmetry and therefore produces statical indetermination to the first degree. If the pipe is not symmetrically loaded with reference to the horizontal axis, only uniaxial symmetry exists. In that case there will be two unknowns and we can set up two simultaneous linear equations whose solution will give us the unknown quantities. The detailed method of this procedure, as well as the general theory of deflection of medium thick, moderately curved, beams is outlined on the succeeding pages. The general scheme of solution for statically indeterminate structures here used was originated by Dr. Müller-Breslau [12], altho, as before noted, the solution of circular rings had previously been accomplished by others, notably Dr. E. Winkler [3] [4] in 1858.

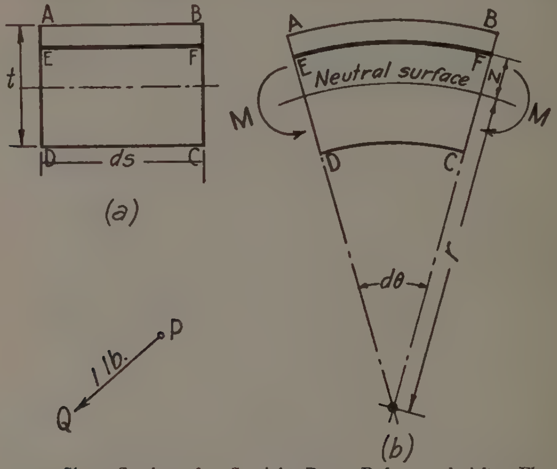


Fig. 13. Short Section of a Straight Beam Before and After Flexure

Figure 13(a) represents a short section of a straight beam (of length ds) before flexure and Figure 13(b) the same section after flexure. Consider a fiber EF, distant z from the neutral surface. After flexure, $ds = rd\theta$, as the length of the neutral surface is unchanged. The new length of $EF = (r + z)d\theta$, and its change in length is therefore $zd\theta$. Its unit deformation is $\frac{zd\theta}{ds}$. If f is unit fiber stress in EF; M, the bending moment, numerically equal to the moment of the other external forces or couples about the point considered, but of opposite sign; and I, the moment of inertia about the neutral axis, of the section, then, from the common theory of flexure, $f = \frac{Mz}{I}$, and if E = modulus of elasticity,

$$E = \frac{f}{\frac{zd\theta}{ds}} \text{ or } f = \frac{Ezd\theta}{ds} = \frac{Mz}{I} \therefore d\theta = \frac{Mds}{EI} \qquad (5)$$

If we wish to find the deflection of a point P, on the beam, in the direction PQ, we place a unit load at P acting in the direction PQ. This unit load produces a moment (m) in acting upon the segment of beam here used. If m is looked upon as a couple of unit arm, the component forces will be numerically equal to m and the work done by them in rotating through the angle $d\theta$ will be $md\theta = \frac{Mds}{EI}\,m$. This must be equal to the work done by the 1 pound load = 1 pound $\times \delta_1$ or integrating over the length of the beam,

$$\delta = \int_0^L \frac{Mmds}{EI} \tag{6}$$

If the segment is subjected to an axial stress S, its deformation will be:

$\frac{Sds}{AE}$ where A is the area of its cross-section. By a line of reasoning similar to the preceding one, we can prove that

(7) - - $\delta = \int_0^L \frac{s}{AE}\,ds$, where s = axial stress at section produced by the unit load.

In a similar manner we can show that

(8) - - $\delta = \int_0^L \frac{VvNds}{E_s A}$ for the shearing stresses, where V = shear at section, v = shear at section due to unit load, N = a section constant = 1.2 for rectangular sections, and E_s = shearing modulus of elasticity, which is about 0.4E for most materials. The above formulas apply only to medium-thick straight beams and require modification for excessively thick or unusually thin sections or curved beams.

For curved beams, a term must be added to take into account the angular deflection produced by axial stress. See Statically Indeterminate Stresses, pages 32 et seq. [13].

$$\delta = \int_0^L \frac{Smds}{AE\rho} \tag{9}$$

where ρ = radius of curvature of beam.[5]

If the beam is thick in comparison to the radius of curvature, the neutral surface will not be at the center of the section, but at some distance, z, from the center, toward the concave side. According to Boyd [14] this distance is

$$z = R_i - \frac{d}{2} - \frac{d}{\log \frac{R_i + d}{R_i}} \tag{10}$$

where d = thickness of beam and R_i = intradosal radius. See Strength of Materials, pages 323 et seq. [14]. The variation in stress is no longer linear across the cross-section, even tho the material follows Hookes Law; because the intradosal fibers are shorter than the others. Even assuming that sections plane before bending remain plane after bending, at any section the total deformations will vary as the distance from the neutral surface, but the unit deformations and consequently the unit stresses, will not vary linearly. For the cases considered herein, this displacement of the neutral surface does not appreciably affect the moment of inertia and consequently it does not affect the deflection, bending, or moments at any section. It does, however, produce a small effect on the unit stresses in the extreme fibers, so that the usual linear law of stress variation can not be accurately used.

---

[5] More accurately $\int_0^L \frac{\mathbf{S}\mathbf{s}ds}{AE}$, where $\mathbf{S} = S - \frac{M}{\rho}$ and $\mathbf{s} = s - \frac{m}{\rho}$. See Müller-Breslau [12]. However, the term as given by Eq. (9) is sufficiently accurate for most cases.

Dr. A. Föppl and Dr. L. Föppl [11] have derived this displacement of the neutral axis by the more rigorous methods of elasticity and have shown agreement with Formula (10) just preceding. They have indicated the possibility of a rigorous solution for pipe under external loads by Airy's stress functions, but for any case, except the very simplest one of uniform external pressure, the process of solution becomes extremely involved.

The 30-inch concrete drain tile in which the stresses were measured (pages 14-19) was made of high quality concrete, and Hookes Law [15] can be assumed to hold true for such material without appreciable error. This is evident from an inspection of Figure 10. For concrete of low strength, a considerable deviation from Hookes Law occurs and corresponding corrections must be made.

To summarize, then, the deflection at any point in any given direction due to bending, axial stress, and shear is

$$\delta = \int_0^L \frac{Mmds}{EI} + \int_0^L \frac{Ssds}{EA} + \int_0^L \frac{VvNds}{Es\,A} + \int_0^L \frac{Smds}{AE\rho} \qquad (11)$$

and if we have a framework of a number of members, we sum up their separate effects. It is possible, also, to add terms for the effects of temperature, shrinkage, and yielding supports.

Application to Statically Indeterminate Structures

Let X_a, X_b, X_c - - - X_n be redundant stresses or reactions in a structure statically indeterminate to the n^{th} degree. Let δ_a, δ_b, δ_c - - - δ_n be the deflections of the supports, or the relative movement of cut faces of members, where a member is assumed cut, the subscripts throughout this discussion always referring to the same support or member. δ_r will be zero for members in general, the exceptions being cases in which members or supports permit part of the total deflection or deformation to occur without resistance. Let δ'_a, δ'_b, δ'_c, - - - δ'_n be deflections that would occur if redundants were removed. Where redundants are reactions the support is removed, and where redundants are stresses the members are cut. Since the removal of all redundants renders the structure statically determinate, all δ''s can be calculated for a given loading. Let δ_{aa} be the deflection at "a" due to a unit load at "a", and similarly for the other points, δ_{rr} is the deflection at "r" due to a unit load at "r" and δ_{rs} is the deflection at "r" due to a unit load at "s". In the above discussion "unit load" may mean a unit reaction, a pair of unit axial stresses, a pair of unit shearing stresses, two unit couples, etc. With redundant supports a single force or moment is used and for redundant members a pair of opposite forces or couples is used. All quantities like δ_{rs} can be determined, because the redundant forces are not acting. A little study will then show that

$$\left.\begin{array}{ll}\delta_a = \delta'_a + X_a\delta_{aa} + X_b\delta_{ab} + X_c\delta_{ac} \; - - - \; X_n\delta_{an} & (1)\\ \delta_b = \delta'_b + X_a\delta_{ba} + X_b\delta_{bb} + X_c\delta_{bc} \; - - - \; X_n\delta_{bn} & (2)\\ \delta_n = \delta'_n + X_a\delta_{na} + X_b\delta_{nb} + X_c\delta_{nc} \; - - - \; X_n\delta_{nn} & (n)\end{array}\right\} \qquad (12)$$

Maxwell's Theorem of reciprocal deflections, which is proved by considering the work done at each point, assures us that $\delta_{rs}=\delta_{sr}$. Note that if angular deflection is desired, we use a unit couple and as the work done by it in rotating through an angle δ_q is 1 pound x δ_q, all the preceding conclusions remain valid. In (12) we have n independent simultaneous equations containing n unknowns and capable of solution. We may adopt any conventions of signs we choose, provided they are consistent throughout; if any X is negative, we interpret that as meaning that it acts in an opposite sense to the direction of the corresponding unit force. We can now proceed with analyses of each of the bearings under various assumptions as to distribution of loading. For convenience of presentation note that all figures are rotated 90° from the normal position.

MATHEMATICAL ANALYSES

Analysis of Sand Bearing, Uniform Distribution of Load

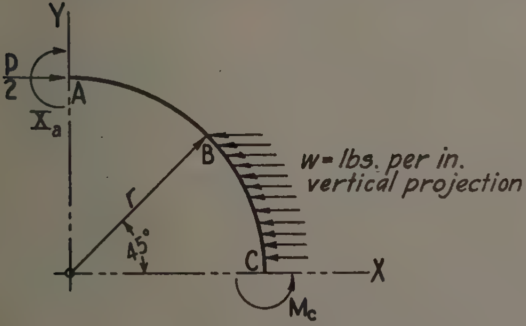


Fig. 14. Uniform Distribution of Load

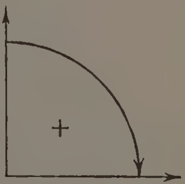


Fig. 15. Convention of Signs

Consider pipe fixed at C and free at A; then X is the only redundant. Owing to symmetry there will be no shear at A and C and no axial stress at C. The forces acting on one quadrant are shown above. Angles θ are measured from the +X axis.

$$M' = \frac{Pr}{2}(1 - \sin\theta) \text{ from A to B and}$$

$$\frac{Pr}{2}(1 - \sin\theta) - \frac{wr^2}{2}\left(\frac{\sqrt{2}}{2} - \sin\theta\right)^2 \text{ from B to C.}$$

$$EI\delta'_a = \int_0^{\pi/2} \frac{Pr^2}{2}(1 - \sin\theta)\,d\theta - \int_0^{\pi/4} \frac{w\,r^3}{2} \left(\frac{1}{2} - \sqrt{2}\sin\theta + \sin^2\theta\right) d\theta$$

$$= \frac{Pr^2}{2}\left(\frac{\pi}{2} - \frac{\pi}{4\sqrt{2}} - \frac{3}{4\sqrt{2}}\right), \text{ noting that } w = \frac{P}{r\sqrt{2}}$$

and considering only deflection produced by bending moments.

$$EI\delta_{aa} = \int_0^{\pi/2} r\,d\theta = \frac{\pi r}{2}$$

$$X_a = -Pr\left(\frac{1}{2} - \frac{1}{4\sqrt{2}} - \frac{3}{4\pi\sqrt{2}}\right) = -.1545\,Pr \qquad (13)$$

$$M_C = -\frac{3}{4\pi\sqrt{2}} = -.1687\,Pr \qquad (14)$$

Analysis of Two-Edge Bearing

Again consider pipe fixed at B and free at A.

Taking a quadrant of the pipe, owing to symmetry there will be no shear at A or B and no axial stress at B.

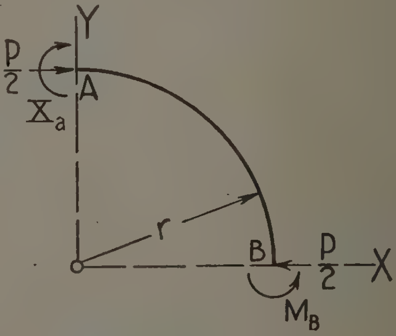


Fig. 16. Two-Edge Bearing

$$M' = \frac{P}{2}(r - y) \text{ or, in polar}$$

co-ordinates,

$$+\frac{Pr}{2}(1 - \sin\theta)$$

$$m_a = 1$$

$$EI\delta'_a = \int_0^{\pi/2} + \frac{Pr^2}{3}(1 - \sin\theta)\,d\theta = +\frac{Pr^2}{2}(\theta + \cos\theta)\Big|_0^{\pi/2} =$$

$$\frac{Pr^2}{2}\left(\frac{\pi}{2} - 1\right)$$

$$\delta_{aa} = \int_0^{\pi/2} ds = \int_0^{\pi/2} r\,d\theta = \frac{\pi r}{2}$$

$$X_a = + \frac{\frac{Pr^2}{2}\left(\frac{\pi}{2} - 1\right)}{\frac{\pi r}{2}} = + Pr\left(\frac{1}{\pi} - \frac{1}{2}\right) = -.1817\, Pr \qquad (15)$$

$$M_B = + Pr\left(\frac{1}{\pi} - \frac{1}{2}\right) - \frac{1}{2} Pr = - \frac{Pr}{\pi} = -.3183\, Pr \qquad (16)$$

Analysis of Three-Edge Bearing

If the pipe is not symmetrically loaded with reference to the horizontal axis, only uniaxial symmetry exists.

The pipe is divided along its axis of symmetry as shown in the figure, and the moment and axial stress at A are considered redundant. After flexure, owing to symmetry, the tangent at A must be parallel to the tangent at C, and δ_a will be zero.

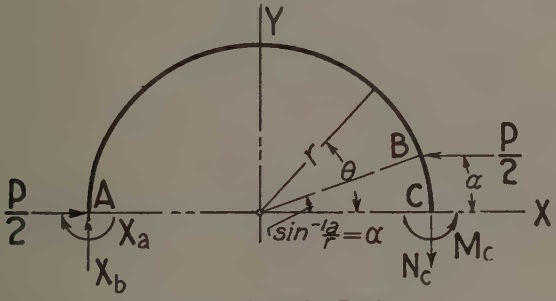


Fig. 17. Three-Edge Bearing

Also A will not deflect parallel to the Y axis, and δ_b will be zero Polar co-ordinates will be used, and the transformation equations are $x = r\cos\theta$, $y = r\sin\theta$, $ds = r\, d\theta$ (θ is measured from $+$ X axis here).

$$M'\,{}^{A}_{B} = -\frac{P}{2} r \sin\theta$$

$$M'\,{}^{B}_{C} = -\frac{Pa}{2}$$

$$EI\delta'_a = \int_{\alpha}^{\pi} -\frac{Pr}{2}\sin\theta\, rd\theta + \int_{0}^{\alpha} -\frac{Pa}{2}\, rd\theta$$

$$= -\frac{Pr^2}{2}\left(-\cos\theta\right)_{\alpha}^{\pi} - \frac{Par}{2}a = -\frac{Pr^2}{2}\left(1 + \cos\alpha\right) - \frac{Par}{2}\alpha$$

$$EI\delta'_b = \int_{\alpha}^{\pi} -\frac{Pr}{2}\sin\theta \,.\, r\,(1 + \cos\theta)\, rd\,\theta + \int_{0}^{\alpha} -\frac{Pa}{2}\, r$$

$$(1 + \cos\theta)\, rd\,\theta$$

$$= -\frac{Pr^3}{2}\left(-\cos\theta + \frac{\sin^2\theta}{2}\right)_{\propto}^{\pi} - \frac{Par^2}{2}(\theta + \sin\theta)_{0}^{\propto}$$

$$= -\frac{Pr^3}{2}\left(1 + \cos\propto - \frac{\sin^2\propto}{2}\right) - \frac{Par^2}{2}(\propto + \sin\propto)$$

$$EI\delta_a = 0 = -\frac{Pr^2}{2}(1 + \cos\propto) - \frac{Par}{2}\propto + \pi r X_a + \pi r^2 X_b$$

$$EI\delta_b = 0 = -\frac{Pr^3}{2}\left(1 + \cos\propto - \frac{\sin^2\propto}{2}\right) - \frac{Par^2}{2}(\propto + \sin\propto) + \pi r^2 X_a + \frac{3}{2}\pi r^3 X_b$$

$$0 = \frac{Pr^2}{4}\sin^2\propto - \frac{Par}{2}\sin\propto + \frac{1}{2}\pi r^2 X_b$$

$$X_b = -\frac{P}{2\pi}\left(\sin^2\propto - 2\frac{a}{r}\sin\propto\right) = +\frac{Pa^2}{2\pi r^2}$$

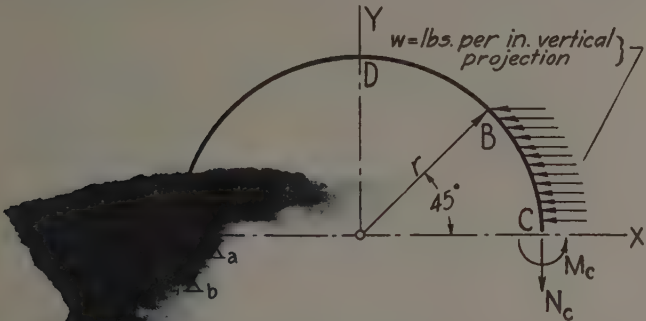
$$X_a = \frac{P}{2\pi r}\left(r^2 + r\sqrt{r^2 - a^2} + ar\propto - a^2\right)$$

$$= \frac{Pr}{2\pi}\left(1 + \sqrt{1 - \frac{a^2}{r^2}} + \frac{a}{r}\alpha - \frac{a^2}{r^2}\right)$$

$$= \frac{Pr}{2\pi}\left[\left(1 - \frac{a^2}{r^2}\right)^{3/2} + \frac{a}{r}\sin^{-1}\frac{a}{r}\right] \qquad (17)$$

This equation (17) is not susceptible of very much simplification even when the usual value of ½ inch is substituted for "a". For large tile the difference in moments between two-edge and three-edge bearings is negligible, and for small tile (12 inches in diameter or less) the effect of the double lower bearing must be separately evaluated for each size of tile. As an indication of the magnitude of this difference, for 6-inch tile, 0.6 inch wall thickness, the maximum moment in the three-edge bearing is 28 per cent less than the corresponding moment for two-edge bearings.

Analysis of Minnesota Bearing, Uniform Distribution of Pressure



Minnesota Bearing—Uniform Distribution of Pressure

Taking half the pipe, owing to symmetry there will be no shear at A or B.

$$w = \frac{P}{r\sqrt{2}}$$

$$M'{}_{A}^{B} = -\frac{Pr}{2}\sin\theta$$

$$M'{}_{B}^{C} = -\frac{Pr}{2}\sin\theta - \frac{w}{2}\left(\frac{r\sqrt{2}}{2} - r\sin\theta\right)^2$$

$$EI\delta'_a = \int_0^{\pi} -\frac{Pr}{2}\sin\theta\, rd\,\theta - \int_0^{\pi/4}\frac{wr^2}{2}\left(\frac{1}{2} - \sqrt{2}\sin\theta + \sin^2\theta\right) rd\,\theta$$

$$= -\frac{Pr^2}{2}(-\cos\theta)_0^{\pi} - \frac{wr^3}{2}\left(\frac{\theta}{2} + \sqrt{2}\cos\theta + \frac{\theta}{2} - \frac{1}{4}\sin 2\,\theta\right)_0^{\pi/4}$$

$$= -\frac{Pr^2}{2}(2) - \frac{wr^3}{2}\left(\frac{\pi}{8} + 1 + \frac{\pi}{8} - \frac{1}{4} - \sqrt{2}\right)$$

$$= -Pr^2 - \frac{Pr^2}{2\sqrt{2}}\left(\frac{\pi}{8} + 1 + \frac{\pi}{8} - \frac{1}{4} - \sqrt{2}\right.$$

$$= -Pr^2\left(1 + \frac{\pi}{8\sqrt{2}} + \frac{3}{8\sqrt{2}} - \frac{1}{2}\right) = -Pr^2\left(\frac{1}{2} + \frac{\pi}{8\sqrt{2}} + \frac{3}{8\sqrt{2}}\right)$$

$$EI\delta'_b = \int_0^{\pi} -\frac{Pr}{2}\sin\theta\,(1 + \cos\theta)\, r^2\, d\,\theta - \int_0^{\pi/4}\frac{wr^2}{2}\left(\frac{1}{2} - \sqrt{2}\sin\theta + \sin^2\theta\right)(1 + \cos\theta)\, r^2 d\theta$$

$$= \int_0^{\pi} -\frac{Pr^3}{2}(\sin\theta + \sin\theta\cos\theta)\, d\theta$$

$$-\int_0^{\pi/4}\frac{wr^4}{2}\left(\frac{1}{2}-\sqrt{2}\sin\theta+\sin^2\theta+\frac{\cos\theta}{2}\right.$$

$$\left.-\sqrt{2}\sin\theta\cos\theta+\sin^2\theta\cos\theta\;d\theta\right.$$

$$=-\frac{Pr^3}{2}\left[-\cos\theta+\frac{\sin^2\theta}{2}\right]_0^{\pi}-\frac{wr^4}{2}\left[\frac{\theta}{2}+\sqrt{2}\cos\theta+\frac{\theta}{2}\right.$$

$$-\frac{1}{4}\sin 2\theta+\frac{\sin\theta}{2}-\sqrt{2}\,\frac{\sin^2\theta}{\text{[illegible]}}\ \text{[illegible]}$$

$$=-\frac{Pr^3}{2}(1+1)-\frac{wr^4}{2}\left(\frac{\pi}{4}+1-\frac{1}{4}-\sqrt{\ }\ \text{[illegible]}\right.$$

$$\left.\frac{\sqrt{2}}{4}-\frac{\sqrt{2}}{4}+\frac{\sqrt{2}}{12}\right)$$

$$=-Pr^3-\frac{wr^4}{2}\left(\frac{\pi}{4}+\frac{3}{4}-\frac{11}{12}\sqrt{2}\right)$$

$$=-Pr^3\left(\frac{13}{24}+\frac{\pi}{8\sqrt{2}}+\frac{3}{8\sqrt{2}}\right)$$

$$EI\delta_a=0=-Pr^2\left(\frac{1}{2}+\frac{\pi}{8\sqrt{2}}+\frac{3}{8\sqrt{2}}\right)+\pi rX_a+\pi r^2X_b$$

$$EI\delta_b=0=-Pr^3\left(\frac{13}{24}+\frac{3}{8\sqrt{2}}+\frac{\pi}{8\sqrt{2}}\right)+\pi r^2X_a+\frac{3}{2}\pi r^3X_b$$

$$0=-Pr^2\left(\frac{1}{24}\right)+\frac{1}{2}\pi r^2X_b$$

$$X_b=\frac{P}{12\pi}=+.0265\ P$$

$$\pi rX_a=Pr^2\left(\frac{1}{2}+\frac{\pi}{8\sqrt{2}}+\frac{3}{8\sqrt{2}}\right)-\frac{Pr^2}{12}=Pr^2\left(\frac{5}{12}+\right.$$

$$\left.\frac{\pi}{8\sqrt{2}}+\frac{3}{8\sqrt{2}}\right)$$

$$X_a=\frac{Pr}{\pi}\left(\frac{5}{12}+\frac{\pi}{8\sqrt{2}}+\frac{3}{8\sqrt{2}}\right)=+.3054\ Pr \qquad (18)$$

$$M_C=-.1815\ Pr$$

$$M_D=+.1682\ Pr \qquad (18a)$$

Analysis of Sand Bearing, Parabolic Distribution of Pressure

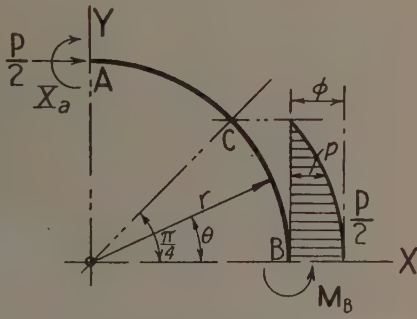


Fig. 19. Sand Bearing—Parabolic Distribution of Pressure

Taking a quadrant, as before, owing to symmetry there will be no shear at A or B and no axial at B.

The equation of a parabola referred to its vert[illegible] $y^2 = cx$ when or[illegible] in Fig. 19. Ins[illegible] y [illegible] x, let us write p, intensit[illegible] y [illegible]ssure, and note that wher[illegible] $\frac{r}{2}\sqrt{2}$, $p = 0$ or $x = \phi - p = \phi$, where ϕ is the maximum intensity of pressure.

$$\frac{r^2}{2} = c\,(\phi) \text{ or } c = \frac{r^2}{2\phi} \therefore y^2 = \frac{r^2}{2\phi}(\phi - p)$$

$$2\phi\,\frac{y^2}{r^2} = \phi - p \text{ or } p = \phi\left(1 - \frac{2y^2}{r^2}\right)$$ is the equation of pressure distribution. This may also be written, since $\frac{y}{r} = \sin\theta$,

$$p = \phi\,(1 - 2\sin^2\theta)$$

The area of the pressure diagram $= \frac{P}{2} = \frac{2}{3} \cdot \phi \cdot \frac{2}{r}\sqrt{2}$ or

$$\phi = \frac{3\sqrt{2}}{4}\frac{P}{r}. \quad \text{Thus } p = \frac{3\sqrt{2}}{4}\frac{P}{r}(1 - 2\sin^2\theta)$$

$$M' = \frac{P}{2}r\,(1 - \sin\theta) \text{ from } \frac{\pi}{4} \text{ to } \frac{\pi}{2} \text{ and } (dy = r\cos\theta\,d\theta)$$

$$M' = \frac{Pr}{2}(1 - \sin\theta) - \int_{\theta}^{\pi/4} p\,(\sin\theta_1 - \sin\theta)\,r^2\cos\theta_1\,d\theta_1$$

$$= \frac{Pr}{2}(1 - \sin\theta) - {}_{\theta}^{\pi/4}\,\frac{3\sqrt{2}}{4}Pr\,(1 - 2\sin^2\theta_1)$$

$$(\sin\theta_1 - \sin\theta)\cos\theta_1\,d\theta_1$$

$$= \frac{Pr}{2}(1 - \sin\theta) - \frac{3\sqrt{2}}{4}Pr\int_{\theta}^{\pi/4}(\sin\theta_1\cos\theta_1 - \sin\theta\cos\theta_1$$

$$-2\sin^3\theta_1\cos\theta_1 + 2\sin^2\theta_1\cos\theta_1\sin\theta)\,d\theta_1$$

$$= \frac{Pr}{2}(1 - \sin\theta) - \frac{3\sqrt{2}}{4}Pr\left(\frac{1}{8} - \frac{\sqrt{2}}{3}\sin\theta + \frac{\sin^2\theta}{2} - \frac{\sin^4\theta}{6}\right)$$

from 0 to $\frac{\pi}{4}$

$$EI\delta'_a = \int_0^{\pi/2} \frac{Pr^2}{2}(1 - \sin\theta)\,d\theta - \int_0^{\pi/4} \frac{3\sqrt{2}}{4} Pr^2 \left(\frac{1}{8} - \frac{\sqrt{2}}{3} \sin\theta + \frac{\sin^2\theta}{2} - \frac{\sin^4\theta}{6}\right) d\theta$$

$$= \frac{Pr^2}{2}\left(\frac{\pi}{2} - 1\right) - \frac{3\sqrt{2}}{4} Pr^2 \left(\frac{5\pi}{64} - \frac{\sqrt{2}}{3} + \frac{1}{4}\right) = \frac{Pr^2}{2}\left(\frac{3}{2} - \frac{15\pi\sqrt{2}}{128} - \frac{3\sqrt{2}}{8}\right)$$

$$EI\delta_{aa} = \int_0^{\pi/2} + r\,d\theta = + \frac{\pi r}{2}$$

$$\therefore X_a = -\frac{\delta'_a}{\delta_{aa}} = -Pr\left(\frac{1}{2} - \frac{15\sqrt{2}}{128} - \frac{3\sqrt{2}}{8\pi}\right) = -.1655\,Pr \qquad (19)$$

$$M_B = -\left[X_a + \frac{Pr}{2} - \left(\frac{3\sqrt{2}}{16}\right)\frac{Pr}{2}\right] = -Pr\left(\frac{3\sqrt{2}}{128} + \frac{3\sqrt{2}}{8\pi}\right)$$

$$= -.2020\,Pr \qquad (20)$$

Analysis of Minnesota Bearing, Parabolic Distribution of Pressure

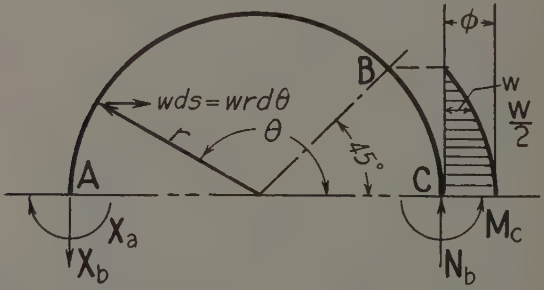


Fig. 20. Minnesota Bearing—Parabolic Distribution of Pressure

From the analysis for sand bearing, $p = \frac{3\sqrt{2}}{4}\frac{P}{r}(1 - 2\sin^2\theta)$

$M' = \frac{Pr}{2}\sin\theta$ from π to $\frac{\pi}{4}$ and

$$= \frac{Pr}{2}\sin\theta + \frac{3\sqrt{2}}{4} Pr \left(\frac{1}{8} - \frac{\sqrt{2}}{3}\sin\theta + \frac{\sin^2\theta}{2} - \frac{\sin^4\theta}{6}\right)$$

from $\frac{\pi}{4}$ to 0

$$EI\delta'_a = + \int_0^\pi M' m_a ds \quad m_a = 1 \quad m_b = (1 + \cos\theta)\ r \quad ds = rd\,\theta$$

$$= \int_0^\pi \frac{Pr^2}{2} \sin\theta\ d\theta + \int_0^{\pi/4} \frac{3\sqrt{2}}{4} Pr^2 \left(\frac{1}{8} - \frac{\sqrt{2}}{3} \sin\theta + \frac{\sin^2\theta}{2} - \frac{\sin^4\theta}{6} \right) d\theta$$

$$= \frac{Pr^2}{2} \left(1 + \frac{3\sqrt{2}}{8} + \frac{15\pi\sqrt{2}}{128} \right)$$

$$EI\delta'_b = \int_0^\pi \frac{Pr^3}{2} \sin\theta\ (1 + \cos\theta)\ d\theta + \int_0^{\pi/4} \frac{3\sqrt{2}\ Pr^3}{4} \left(\frac{1}{8} - \frac{\sqrt{2}}{3} \sin\theta + \frac{\sin^2\theta}{2} - \frac{\sin^4\theta}{6} \right) (1 + \cos\theta)\ d\theta$$

$$= -\frac{Pr^3}{2} \left(\frac{21}{20} + \frac{3\sqrt{2}}{8} + \frac{15\pi\sqrt{2}}{128} \right)$$

$$EI\delta_{bb} = \int_0^\pi m^2_a\ ds = \int_0^\pi (1 + \cos\theta)^2\ r^3\ d\theta = \frac{3}{2}\pi r^3$$

$$EI\delta_{ab} = EI\delta_{ba} = \int_0^\pi r^2\ (1 + \cos\theta)\ d\theta = + \pi r^2$$

$$EI\delta_{aa} = \int_0^\pi rds = \pi r$$

$$\left. \begin{aligned} EI\delta'_a = 0 &= -\frac{Pr^2}{2} \left(1 + \frac{3\sqrt{2}}{8} + \frac{15\pi\sqrt{2}}{128} \right) + \pi r^2 X_b + \pi r X_a \\ EI\delta'_b = 0 &= -\frac{Pr^3}{2} \left(\frac{21}{20} + \frac{3\sqrt{2}}{8} + \frac{15\pi\sqrt{2}}{128} \right) + \frac{3}{2}\pi r^3 X_b + \pi r^2 X_a \end{aligned} \right\}$$

Solving these two simultaneous equations,

$$X_a = + Pr \left(\frac{9}{20\pi} + \frac{3\sqrt{2}}{16\pi} + \frac{15\sqrt{2}}{256} \right) = + .3105\ Pr \qquad (21)$$

$$X_b = + \frac{P}{20\pi} = .0159\ P \qquad (22)$$

$$M_B = -.2096\ Pr \qquad (23)$$

$$M_D = + .1737\ Pr \qquad (24)$$

Stresses Due to Own Weight, Two-Edge Bearing

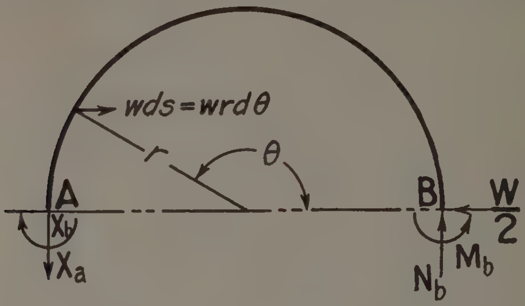


Fig. 21. Stresses Due to Own Weight—Two-Edge Bearing

$W =$ weight of tile

$w =$ weight per unit of circumference

$$w = \frac{W}{2\pi r}$$

$$M' = \int_{\theta}^{\pi} - wr^2 (\sin\theta - \sin\theta')\, d\theta$$

$$= \int_{\theta}^{\pi} \frac{Wr}{2\pi} (\sin\theta' - \sin\theta)\, d\theta$$

$$= \frac{Wr}{2\pi} (1 + \theta\sin\theta + \cos\theta - \pi\sin\theta)$$

$$m_a = +1 \qquad m_b = -r(1 + \cos\theta)$$

$$EI\delta'_a = \int_{0}^{\pi} \frac{Wr^2}{2\pi} (-\pi\sin\theta + 1 + \theta\sin\theta + \cos\theta)\, d\theta = 0$$

$$EI\delta'_b = \frac{Wr^3}{2\pi} \int_{0}^{\pi} (\pi\sin\theta - 1 - \theta\sin\theta - \cos\theta)(1 + \cos\theta)\, d\theta = \frac{Wr^3}{8}$$

$$EI\delta_{aa} = \pi r, \qquad EI\delta_{ab} = -\pi r^2$$

$$EI\delta_{bb} = \frac{3}{2}\pi r^3$$

$$EI\delta_a = 0 = 0 + \pi r X_a - \pi r^2 X_b$$

$$EI\delta_b = 0 = -\frac{Wr^2}{8} - \pi r^2 X_a + \frac{3}{2}\pi r^3 X_b$$

Solving these two simultaneous equations,

$$X_a = +\frac{Wr}{4\pi} = +.0795\, Wr \tag{25}$$

$$X_b = +\frac{W}{4\pi} = +.0795\, W \tag{26}$$

$$M_B = \frac{3Wr}{4\pi} = .2385\,Wr \qquad (27)$$

This is 3/4 of the moment produced by opposed diametral loads P.

Stresses Due to Own Weight, Sand and Minnesota Bearings

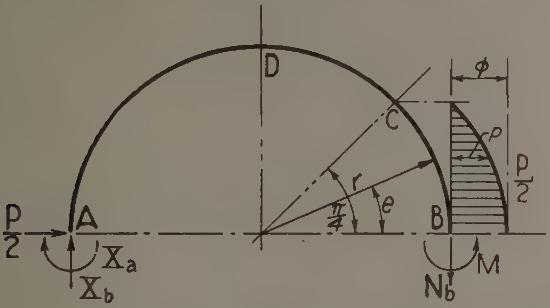


Fig. 22. Stresses Due to Own Weight, Sand and Minnesota Bearings

W = weight of tile

w = weight per unit of circumference

w′ = unit pressure on lower bearing

$$w = \frac{W}{2\pi r}$$

$$w' = \frac{3\sqrt{2}}{4}\frac{W}{r}(1 - 2\sin^2\theta) \text{ (assuming parabolic distribution)}$$

(see p. 34.)

$$M' = \int_{\theta}^{\pi} - wr\,(\sin\theta - \sin\theta')\,rd\theta' \Big]_{0}^{\pi} + \int_{\theta}^{\pi/4} - w'r\,(\sin\theta' - \sin\theta)\,rd\theta' \Big]_{0}^{\pi/4}$$

$$= \frac{Wr}{2\pi}\int_{\theta}^{\pi} - (\sin\theta - \sin\theta')\,d\theta' \Big]_{0}^{\pi} + \frac{3\sqrt{2}}{4}Wr\int_{\theta}^{\pi/4} - (1 - 2\sin^2\theta')\,(\sin\theta' - \sin\theta)\,d\theta' \Big]_{0}^{\pi/4}$$

$$= \frac{Wr}{2\pi}(-\pi\sin\theta + 1 + \theta\sin\theta + \cos\theta) \Big]_{0}^{\pi} + \frac{3\sqrt{2}}{4}Wr\left(-\frac{\sqrt{2}}{3} + \frac{1}{2}\sin\theta + \frac{1}{3}\cos^3\theta\right)\Big]_{0}^{\pi/4}$$

$m_a = +1 \qquad m_b = -r\,(1 + \cos\theta)$

$$EI\delta'_a = \int_0^\pi M'm_a ds = \int_0^\pi \frac{Wr^2}{2\pi}(\pi \sin\theta - 1 - \theta\sin\theta - \cos\theta)\, d\theta$$

$$+ \int_0^{\pi/4} \frac{3\sqrt{2}}{4} Wr^2 \left(\frac{\sqrt{2}}{3} - \frac{1}{2}\sin\theta - \frac{1}{3}\cos^3\theta\right) d\theta$$

$$= Wr^2\left(\frac{\pi}{8} + \frac{1}{6} - \frac{3}{8}\sqrt{2}\right) = .0291\ Wr^2$$

$$EI\delta'_b = \int_0^\pi M'm_b ds = \int_0^\pi \frac{Wr^3}{2\pi}(\pi\sin\theta - 1 - \theta\sin\theta - \cos\theta)$$

$$(1 + \cos\theta)\, d\theta + \int_0^{\pi/4} \frac{3\sqrt{2}}{4} Wr^3 \left(\frac{\sqrt{2}}{3}\right.$$

$$\left. - \frac{1}{2}\sin\theta - \frac{1}{3}\cos^3\theta\right)(1 + \cos\theta)\, d\theta$$

$$= Wr^3\left(\frac{\pi}{8} + \frac{1}{24} - \frac{9\sqrt{2}}{32} - \frac{3\pi\sqrt{2}}{128}\right) = -\ .0675\ Wr^3$$

$$EI\delta_{aa} = \pi r, \qquad EI\delta_{ab} = EI\delta_{ba} = \pi r^2, \qquad EI\delta_{bb} = \frac{3}{2}\pi r^3,$$

$$0 = -\ .0291\ Wr^2 + \pi r X_a - \pi r^2 X_b$$

$$0 = -\ .0675\ Wr^3 - \pi r^2 X_a + \frac{3}{2}\pi r^3 X_b$$

Solving these two simultaneous equations,

$$X_a = +\ .0707\ Wr \tag{28}$$

$$X_b = +\ .0614\ W \tag{29}$$

$$M_C = -\ .1197\ Wr \tag{30}$$

Deformation of Vertical Diameter Two-Edge Bearing

$$M_A = -\ Pr\left(\frac{1}{2} - \frac{1}{\pi}\right),$$

$$M_B = -\frac{Pr}{\pi}$$

$$M = -\ Pr\left(\frac{\sin\theta}{2} - \frac{\pi}{1}\right),$$

$$m = -\ r\left(\frac{\sin\theta}{2} - \frac{1}{\pi}\right)$$

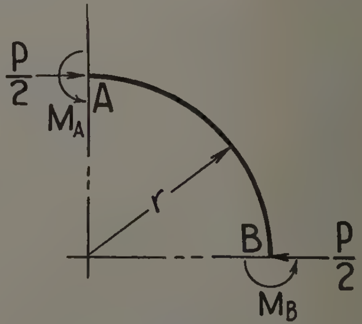


Fig. 23. Deformation of Vertical Diameter—Two-Edge Bearing

$$N = \frac{P}{2}\sin\theta, \qquad n = \frac{\sin\theta}{2}\,;\, n + \frac{m}{r} = \left(\frac{\sin\theta}{2} - \frac{\sin\theta}{2} + \frac{1}{\pi}\right) = \frac{1}{\pi}$$

$$V = \frac{P}{2}\cos\theta, \qquad v = \frac{\cos\theta}{2}$$

$$\frac{1}{4}E\delta_v = \int_0^{\pi/2} \frac{Pr}{I}\left(\frac{\sin\theta}{2} - \frac{1}{\pi}\right) r \left(\frac{\sin\theta}{2} - \frac{1}{\pi}\right) r d\theta$$

$$+ \int_0^{\pi/2} \frac{Pr}{A}\,\frac{\sin^2\theta}{2\pi}\,d\theta + \int_0^{\pi/2} \frac{3Pr}{A} \cdot \frac{\cos^2\theta}{4}\,d\theta^*$$

$$E\delta_v = \frac{Pr^3}{I}\left(\frac{\pi}{4} - \frac{2}{\pi}\right) + \frac{Pr}{A}\left(\frac{3\pi}{4} + \frac{2}{\pi}\right) \tag{31}$$

$$^*\text{ Note: } \int \frac{1.2\,Vvds}{E_sA} = \int \frac{1.2\,Vvds}{.4EA} = \int \frac{3\,Vvds}{EA}$$

Assuming $E_s = .4E$ or μ (Poisson's number) $= 4$

Deformation of Vertical Diameter Sand Bearing

(See Figure 19.)

$$X_a = Pr\left(\frac{1}{2} - \frac{15\sqrt{2}}{128} - \frac{3\sqrt{2}}{8\pi}\right)$$

$$M = Pr\left(\frac{15\sqrt{2}}{128} - \frac{3\sqrt{2}}{8\pi} - \frac{1}{2}\sin\theta\right) \text{from A to C, and}$$

$$M = Pr\left(\frac{15\sqrt{2}}{128} - \frac{3\sqrt{2}}{8\pi} - \frac{1}{2}\sin\theta\right) - \frac{3\sqrt{2}}{4}Pr\left(\frac{1}{8} - \frac{\sqrt{2}}{3}\sin\theta + \frac{\sin^2\theta}{2} - \frac{\sin^4\theta}{6}\right) \text{from C to B}$$

$$N = \frac{P}{2}\sin\theta \text{ from A to C, and}$$

$$N = \frac{P}{2}\sin\theta - \frac{3\sqrt{2}}{4}P\left(\frac{\sqrt{2}}{3}\sin\theta - \sin^2\theta + \frac{2}{3}\sin^4\theta\right) \text{from C to B}$$

$$V = \frac{P}{2}\cos\theta \text{ from A to C and}$$

$$V = \frac{P}{2}\cos\theta - \frac{3\sqrt{2}}{4}P\left(\frac{\sqrt{2}}{3}\cos\theta - \sin\theta + \frac{2}{3}\sin^3\theta\cos\theta\right)$$

from C to B

108486

m, n, and v are the same as for Two-edge Bearing

$$\frac{1}{4}E\delta_v = \int_0^{\pi/2}\frac{M\,m\,ds}{I} + \int_0^{\pi/2}\frac{N(n + m/r)ds}{A} + \int_0^{\pi/2}\frac{3\,V\,v\,ds}{A}$$

Substituting the quantities above for M, N and V and integrating between the proper limits, we get,

$$E\delta_v = \frac{Pr}{I}\left(\frac{\pi}{8} + \frac{307\sqrt{2}}{960} - \frac{3\sqrt{2}}{4\pi} - \frac{23}{60}\right) + \frac{Pr}{A}\left(\frac{103\sqrt{2}}{80} + \frac{3\sqrt{2}}{4\pi} + \frac{3\pi}{8} - \frac{23}{20}\right) \qquad (32)$$

Deformation of Vertical Diameter Minnesota Bearing

(See Figure 20.)

$$X_a = Pr\left(\frac{9}{20\pi} + \frac{3\sqrt{2}}{16\pi} + \frac{15\sqrt{2}}{256}\right)$$

$$X_b = \frac{P}{20\pi}$$

$$M = Pr\left(\frac{\cos\theta}{20\pi} - \frac{\sin\theta}{2} + \frac{1}{2\pi} + \frac{3\sqrt{2}}{16\pi} + \frac{15\sqrt{2}}{256}\right) \text{from 0 to } \frac{1}{4}\pi \text{ (A to C)}$$

$$M = Pr\left(\frac{\cos\theta}{20\pi} - \frac{\sin\theta}{2} + \frac{1}{2\pi} + \frac{3\sqrt{2}}{16\pi} + \frac{15\sqrt{2}}{256}\right) - \frac{3\sqrt{2}}{4}Pr\left(\frac{1}{8} - \frac{\sqrt{2}}{3}\sin\theta + \frac{\sin^2\theta}{2} - \frac{\sin^4\theta}{6}\right) \text{from C to B}$$

$$N = \frac{P}{2}\sin\theta - \frac{P}{20\pi}\cos\theta \text{ from A to C and}$$

$$N = \frac{P}{2}\sin\theta - \frac{P}{20\pi}\cos\theta - \frac{3\sqrt{2}}{4}P\left(\frac{\sqrt{2}}{3}\sin\theta - \sin^2\theta + \frac{2}{3}\sin^4\theta\right) \text{from C to B}$$

$$V = \frac{P}{2}\cos\theta + \frac{P}{20\pi}\sin\theta \text{ from A to C and}$$

$$V = \frac{P}{2}\cos\theta + \frac{P}{20\pi}\sin\theta - \frac{3\sqrt{2}}{4}P\left(\frac{\sqrt{2}}{3}\cos\theta - \sin\theta\cos\theta + \frac{2}{3}\sin^3\theta\cos\theta\right) \text{from C to B}$$

m, n and v are the same as before, for Sand and Two-edge Bearing

$$\frac{1}{2}E\delta_v = \int_0^\pi \frac{M\,m\,ds}{I} + \int_0^\pi \frac{N(n + m/r)ds}{A} + \int_0^\pi \frac{3\,V\,v\,ds}{A}$$

Substituting the above quantities in the last equation and integrating between the proper limits, we get,

$$E\delta_v = \frac{Pr^3}{I}\left(\frac{3\pi}{16} - \frac{1}{\pi} + \frac{307\sqrt{2}}{1920} - \frac{3\sqrt{2}}{8\pi} - \frac{23}{120}\right) + \frac{Pr}{A}\left(\frac{9\pi}{16} - \frac{23}{40} + \frac{103\sqrt{2}}{160} + \frac{1}{\pi}\frac{3\sqrt{2}}{8\pi}\right) \tag{33}$$

PRESSURE DISTRIBUTION ON CIRCULAR PIPE UNDER LOAD IN SAND BEARINGS AS MEASURED BY FRICTION STRIPS

The method here used to determine the distribution of pressure in the sand bearings is described in detail in the 1926 Proceedings of the American Society for Testing Materials [17] and is based on a well known law of physics that for specific materials the initial force required to overcome static friction is proportional to the load. This law of physics was applied, in this work, by measuring, in pounds, the starting pull required to move steel strips laid between pieces of 10-ounce canvas placed between the sand of the bearings and the outer circumference of a circular pipe of 26 inches outside diameter. (See Fig. 24.)

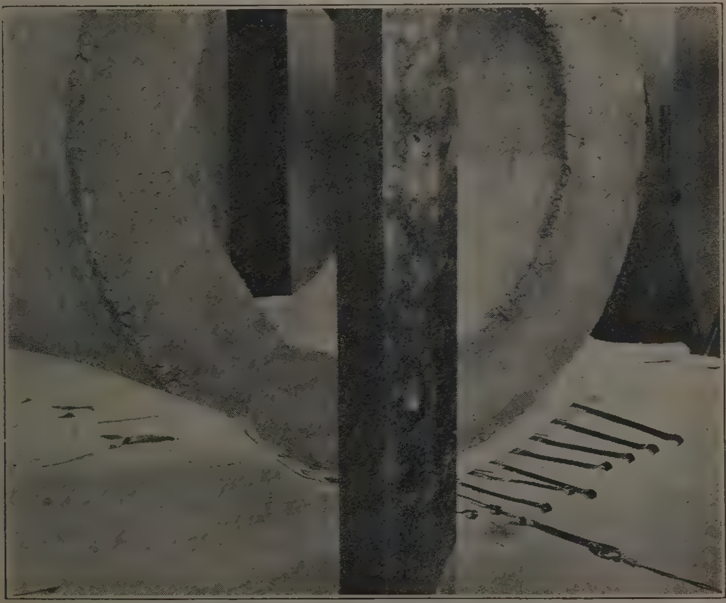


Fig. 24. Steel Strips in Place as Used in Determining the Pressure Distribution in the Lower Bearing of the A.S.T.M. Standard Sand Bearing

In the studies made with this pipe, 15 steel strips 5/16 inch in width and 1/64 inch thick were used. It was found in all cases that in order to obtain consistent results it was necessary that the area between the strips be covered as nearly as possible by auxiliary strips of the same thickness as those pulled, else when the sand became compacted beyond a certain degree the strips took a proportion of the load in excess of that calculated for their combined areas.

The pull, in pounds, on each strip was measured by means of a spring balance working through a lever arm with a 1:5 ratio. By using the lever arm rather than pulling direct, it was possible to control the tendency of a strip to jump an inch or two when started, while a single strip could in this way be started and the scale consistently read as many as thirty times without more than a slight displacement of the strip.

The 15 strips were equally spaced, as indicated in Figure 25, with reference to the 17-inch chord, 11/16 inch center to center. The two end strips, however, were 11/16 inch from the extremities of this chord so that the actual area, on the cord, represented by each end strip is 50 per cent in excess of the other strips. The load on this excess area, coming as it does at the edge of the sand, was too small to measure and in the calculations has been neglected.

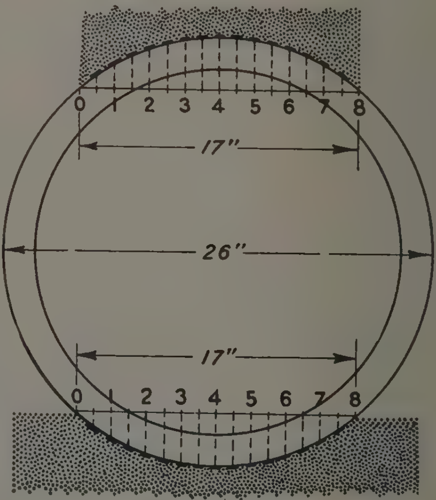


Fig. 25. Position of 5/16-Inch Steel Strips for Measuring the Distribution of Pressure at the Top and Bottom Sand Bearings
The strips are equally spaced with reference to the 17-inch chord.

In Tables VIII and IX, in the third line of each loading under the various bedding conditions, are recorded, as calculated from the pull on the strips, the actual load reduced to loads on sections, corresponding to respective strips, per linear inch of tile. These are the data upon which the graphs of Figures 26 and 27 are based, the loads being reduced, in the figures, to pressure in pounds per square inch. Note that this pressure is with reference to the horizontal projection of the quadrant of the pipe in contact with the sand as represented by the 17-inch cord of Figure 25.

TABLE VIII

Distribution of Pressure in the Lower Sand Bearing of a 24-Inch Tile Under Loads of 1080, 2500, and 3500 Pounds per Linear Foot

Under each loading the first line is the average pull of two independent sets of readings, the second line is the average of corresponding readings on the two sides of the center strip, while the data in the third line are those of line 2 reduced to loads on sections, corresponding to respective strips, per linear inch of tile. Each section, therefore, measures 1 by 1 1/16 inches

ROOM DRY SAND (0.45 PER CENT MOISTURE)

Load on tile, per linear ft.	Strips as Numbered															
	½	1	1½	2	2½	3	3½	4	4½	5	5½	6	6½	7	7½	Totals
	Bedding No. 1(a) Loose Sand															
lb. 1080	1.25	0.75	8.75	10.62	15.62	27.50	28.75	40.63	26.25	28.37	18.75	11.88	10.00	4.75	0.13	240.00
	0.60	5.73	9.37	11.25	17.18	27.04	27.50	40.03	27.50	27.04	17.18	11.25	9.37	5.73	0.60	230.09
	0.40	3.36	5.45	6.57	10.02	16.30	16.05	23.70	16.05	16.30	10.02	6.57	5.45	3.36	0.40	140.00
2500	2.75	8.74	13.75	18.13	26.25	40.00	40.00	55.00	38.13	40.00	28.75	20.00	16.25	6.88	0.25	351.88
	1.50	7.82	15.00	19.07	27.50	40.00	39.06	55.00	39.06	40.00	27.50	19.07	15.00	7.82	1.50	354.90
	0.88	4.59	8.81	11.19	16.15	23.48	22.93	32.29	22.93	23.48	16.15	11.19	8.81	4.59	0.88	208.35
3500	4.75	15.63	20.00	26.25	37.50	53.13	54.13	73.75	40.37	53.13	30.37	28.75	25.13	11.25	0.50	488.04
	2.03	13.44	21.06	27.50	38.11	53.13	51.25	73.75	51.25	53.13	38.44	27.50	21.06	13.44	2.03	488.03
	1.50	8.02	12.57	16.41	22.01	31.21	30.50	44.02	30.50	31.21	22.01	16.41	12.57	8.02	1.50	291.03
	Bedding No. 2(a) Slightly Compacted Sand															
1080	0.62	5.25	10.00	8.75	12.50	20.63	45.62	40.37	37.50	23.13	12.13	11.37	10.00	6.88	3.75	255.50
	2.10	6.07	10.00	11.56	12.32	21.88	39.06	49.37	39.06	21.88	12.32	11.56	10.00	6.07	2.10	255.53
	1.20	3.33	5.48	6.33	6.73	11.99	21.40	27.06	21.40	11.99	6.73	6.33	5.48	3.33	1.20	140.02
2500	2.25	10.00	18.75	17.50	22.13	30.00	61.88	65.00	41.88	32.50	20.00	21.25	15.63	11.63	5.63	[illegible]
	3.04	10.81	17.19	19.37	21.07	31.25	51.88	65.00	51.88	31.25	21.07	19.37	17.19	10.81	3.04	[illegible]
	2.18	5.99	9.52	10.73	11.07	17.31	28.74	36.01	28.74	17.31	11.07	10.73	9.52	5.99	2.18	208.50
3500	5.25	18.75	30.63	25.13	35.63	43.75	81.25	85.00	56.25	40.25	28.75	30.63	22.13	16.88	10.00	[illegible]
	7.63	17.64	26.37	27.88	32.10	45.00	68.75	85.00	68.75	45.00	32.10	27.88	26.37	17.64	7.63	530.28
	4.15	9.60	14.34	15.16	17.51	24.47	37.30	46.23	37.30	24.47	17.51	15.16	14.34	9.60	4.15	291.65

TABLE VIII—*Continued*

Load on tile, per linear ft.	Strips as Numbered															
	½	1	1½	2	2½	3	3½	4	4½	5	5½	6	6½	7	7½	Totals
lb.																
	Bedding No. 3(a) Thoroly Compacted Sand															
1680	0.75	4.75	9.37	10.00	10.62	25.00	48.13	63.75	47.50	22.50	8.75	6.00	3.87	1.88	0.63	263.50
	0.69	3.32	6.62	8.00	9.68	23.75	47.82	63.75	47.82	23.75	9.68	8.00	6.62	3.32	0.69	263.51
	0.37	1.76	3.52	4.25	5.14	12.62	25.41	33.87	25.41	12.62	5.14	4.25	3.52	1.76	0.37	140.01
2500	2.12	7.62	15.62	17.50	17.50	38.13	68.12	81.88	66.25	35.00	16.25	7.50	6.00	3.50	1.63	384.62
	1.88	5.56	10.81	12.50	16.88	36.57	67.18	81.88	67.18	36.57	16.88	12.50	10.81	5.56	1.88	384.64
	1.02	3.01	5.86	6.77	9.14	19.81	36.39	44.35	36.39	19.81	9.14	6.77	5.86	3.01	1.02	208.35
3500	4.00	11.25	24.13	27.50	28.75	52.50	85.62	101.25	86.25	48.75	26.25	10.62	8.75	6.75	3.00	525.37
	3.50	9.00	16.44	19.06	27.50	50.63	85.94	101.25	85.94	50.63	27.50	19.06	16.44	9.00	3.50	525.39
	1.94	5.00	9.13	10.58	15.27	28.11	47.71	56.21	47.71	28.11	15.27	10.58	9.13	5.00	1.94	291.69
	SAND CONTAINING 2.5 PER CENT MOISTURE Bedding No. 1(b) Loose Sand															
1680	8.00	10.62	14.37	17.50	21.25	18.75	24.37	24.37	24.12	23.13	20.63	15.62	8.75	7.62	5.50	244.60
	6.75	9.12	11.56	16.56	20.94	20.94	24.25	24.37	24.25	20.94	20.94	16.56	11.56	9.12	6.75	244.61
	3.86	5.22	6.62	9.48	11.98	11.98	13.88	13.95	13.88	11.98	11.98	9.48	6.62	5.22	3.86	139.99
2500	11.25	18.75	22.50	25.00	31.88	28.13	36.88	36.88	35.62	36.25	31.88	24.37	13.37	11.25	8.25	372.26
	9.75	15.00	17.94	24.68	31.88	32.19	36.25	36.88	36.25	32.19	31.88	24.68	17.94	15.00	9.75	372.26
	5.46	8.39	10.04	13.81	17.84	18.01	20.29	20.64	20.29	18.01	17.84	13.81	10.04	8.39	5.46	208.32
3500	16.25	25.63	32.50	35.00	45.62	39.37	52.50	51.88	51.25	50.63	46.25	35.63	21.25	18.13	11.88	533.77
	14.06	21.88	26.88	35.32	45.94	45.00	51.88	51.88	51.88	45.00	45.94	35.32	26.88	21.88	14.06	533.80
	7.68	11.95	14.69	19.30	25.10	24.59	28.35	28.35	28.35	24.59	25.10	19.30	14.69	11.95	7.68	291.67

TABLE VIII—*Continued*

Load on tile, per linear ft.	Strips as Numbered															
	½	1	1½	2	2½	3	3½	4	4½	5	5½	6	6½	7	7½	Totals
	Bedding No. 2(b) Slightly Compacted Sand															
1680	0.62	1.25	3.50	13.13	22.50	24.37	41.25	46.25	33.75	21.88	19.37	16.25	4.50	1.50	0.88	251.00
	0.75	1.38	4.00	14.69	20.94	23.12	37.50	46.25	37.50	23.12	20.94	14.69	4.00	1.38	0.75	251.01
	0.42	0.77	2.23	8.19	11.68	12.90	20.92	25.80	20.92	12.90	11.68	8.19	2.23	0.77	0.42	140.02
lb. 2500	0.88	3.63	6.75	22.50	36.25	38.75	55.62	60.63	46.88	34.37	28.75	24.37	7.38	3.00	2.25	372.01
	1.57	3.31	7.06	23.44	32.50	36.56	51.25	60.63	51.52	36.56	32.50	23.44	7.06	3.31	1.57	372.01
	0.88	1.85	3.95	13.13	18.20	20.47	28.70	33.95	28.70	20.47	18.20	13.13	3.95	1.85	0.88	208.31
3500	1.75	7.75	11.88	37.50	51.88	53.13	66.88	70.00	60.63	48.75	43.75	38.75	13.75	6.37	4.50	517.27
	3.13	7.06	12.81	38.13	47.82	50.94	63.75	70.00	63.75	50.94	47.82	38.13	12.81	7.06	3.13	517.28
	1.76	3.98	7.22	21.50	26.96	28.72	35.94	39.47	35.94	28.72	26.96	21.50	7.22	3.98	1.76	291.63
	Bedding No. 3(b) Thoroly Compacted Sand															
1680	0.13	0.12	1.50	9.50	15.00	20.00	55.63	58.13	50.00	34.37	6.75	5.50	3.75	0.63	0.25	261.26
	0.19	0.37	2.62	7.50	10.88	27.19	52.82	58.13	52.82	27.19	10.88	7.50	2.62	0.37	0.19	261.27
	0.10	0.20	1.40	4.02	5.83	14.57	28.30	31.15	28.30	14.57	5.83	4.02	1.40	0.20	0.10	139.99
2500	1.13	1.13	3.88	18.13	26.25	34.37	74.37	68.75	62.50	51.88	12.50	10.50	7.75	1.50	0.88	375.52
	1.00	1.31	5.82	14.31	19.37	43.13	68.44	68.75	68.44	43.13	19.37	14.31	5.82	1.31	1.00	375.51
	0.55	0.73	3.23	7.94	10.75	23.93	37.97	38.14	37.97	23.93	10.75	7.94	3.23	0.73	0.55	208.34
3500	2.75	3.63	9.00	35.00	45.00	54.37	93.75	80.00	78.12	78.75	25.00	20.63	13.75	4.13	2.50	546.38
	2.62	3.88	11.37	27.81	35.00	66.56	85.93	80.00	85.93	66.56	35.00	27.81	11.37	3.88	2.62	546.34
	1.40	2.07	6.07	14.85	18.68	35.53	45.87	42.71	45.87	35.53	18.68	14.85	6.07	2.07	1.40	291.65

TABLE VIII—*Continued*

Load on tile, per linear ft.	Strips as Numbered															
	½	1	1½	2	2½	3	3½	4	4½	5	5½	6	6½	7	7½	Totals
	SAND CONTAINING 5.0 PER CENT MOISTURE Bedding No. 1(c) Loose Sand															
1680	6.00	9.75	11.62	15.00	23.75	25.62	26.25	24.38	26.25	20.00	24.37	18.75	11.25	9.75	7.75	260.49
	6.88	9.75	11.44	16.88	24.06	22.81	26.25	24.38	26.25	22.81	24.06	16.88	11.44	9.75	6.88	260.52
	3.70	5.24	6.15	9.07	12.93	12.26	14.11	13.10	14.11	12.26	12.93	9.07	6.15	5.24	3.70	140.02
2500	9.75	14.37	18.13	25.00	37.50	38.13	38.75	35.00	38.13	28.13	33.75	26.88	18.13	13.13	10.00	384.78
	9.87	13.75	18.13	25.94	35.63	33.13	38.44	35.00	38.44	33.13	35.63	25.94	18.13	13.75	9.87	384.78
	5.34	7.44	9.82	14.04	19.29	17.94	20.81	18.95	20.81	17.94	19.29	14.04	9.82	7.44	5.34	208.31
3500	11.25	20.00	26.25	35.63	55.00	53.13	55.00	47.50	51.25	40.00	50.00	36.88	25.63	17.50	13.13	538.15
	12.19	18.75	25.94	36.25	52.50	46.57	53.13	47.50	53.13	46.57	52.50	36.25	25.94	18.75	12.19	538.16
	6.61	10.16	14.06	19.65	28.45	25.24	28.79	25.74	28.79	25.24	28.45	19.65	14.06	10.16	6.61	291.66
lb.																
	Bedding No. 2(c) Slightly Compacted Sand															
1680	0.63	1.00	3.25	10.00	16.25	30.00	32.50	35.63	34.37	25.00	23.13	23.12	10.63	2.37	0.62	248.50
	0.63	1.69	6.94	16.56	19.69	27.50	33.44	35.63	33.44	27.50	19.69	16.56	6.94	1.69	0.63	248.53
	0.35	0.95	3.91	9.33	11.09	15.49	18.84	20.07	18.84	15.49	11.09	9.33	3.91	0.95	0.35	139.99
2500	1.50	3.25	7.00	16.25	27.50	45.63	45.00	45.63	46.88	44.37	35.00	33.13	15.00	4.00	1.00	371.14
	1.25	3.63	11.00	24.69	31.25	45.00	45.94	45.63	45.94	45.00	31.25	24.69	11.00	3.63	1.25	371.15
	0.70	2.04	6.17	13.86	17.54	25.26	25.79	25.61	25.79	25.26	17.54	13.86	6.17	2.04	0.70	208.33
3500	3.50	7.13	12.50	30.63	45.63	64.37	60.63	60.00	61.88	59.37	46.88	46.25	23.75	7.00	2.37	531.89
	2.94	7.06	18.13	38.44	46.25	61.87	61.25	60.00	61.25	61.87	46.25	38.44	18.13	7.06	2.94	531.88
	1.61	3.87	9.94	21.08	25.36	33.93	33.59	32.90	33.59	33.93	25.36	21.08	9.94	3.87	1.61	291 66

TABLE VIII—*Continued*

Load on tile, per linear ft.	Strips as Numbered														
	½	1	1½	2	2½	3	3½	4	4½	5	5½	6	6½	7	7½	Totals
Bedding No. 3(c) Thoroly Compacted Sand																
1680	0.62	2.00	5.25	10.63	15.63	34.37	38.37	42.50	35.00	30.00	20.63	11.37	5.75	1.37	1.13	254.62
	0.88	1.69	5.50	11.00	18.13	32.18	36.68	42.50	36.68	32.18	18.13	11.00	5.50	1.69	0.88	254.62
	0.48	0.93	3.02	6.05	9.97	17.69	20.17	23.37	20.17	17.69	9.97	6.05	3.02	0.93	0.48	139.99
2500	1.75	4.50	8.87	17.50	26.88	51.88	55.00	60.00	51.25	42.50	32.50	18.75	9.00	2.50	1.62	384.50
	1.68	3.50	8.93	18.13	29.69	47.19	53.13	60.00	53.13	47.19	29.69	18.13	8.93	3.50	1.68	384.50
	0.91	1.90	4.84	9.82	16.09	25.57	28.79	32.51	28.79	25.57	16.09	9.82	4.84	1.90	0.91	208.35
3500	3.25	8.25	15.63	34.37	40.62	70.63	73.12	76.88	68.12	56.88	45.00	29.37	13.75	4.25	2.00	542.12
	2.63	6.25	14.69	31.87	42.81	63.75	70.62	76.88	70.62	63.75	42.81	31.87	14.69	6.25	2.63	542.12
	1.41	3.36	7.90	17.15	23.03	34.30	37.99	41.36	37.99	34.30	23.03	17.15	7.90	3.36	1.41	291.64
SAND CONTAINING 10.0 PER CENT MOISTURE Bedding No. 1(d) Loose Sand																
1680	5.37	7.00	10.62	15.00	21.25	26.88	21.88	26.88	22.88	23.12	23.75	18.75	13.75	9.25	6.50	252.88
	5.94	8.12	12.19	16.88	22.50	25.00	22.38	26.88	22.38	25.00	22.50	16.88	12.19	8.12	5.94	252.90
	3.29	4.50	6.75	9.34	12.46	13.84	12.39	14.88	12.39	13.84	12.46	9.34	6.75	4.50	3.29	140.02
lb. 2500	8.00	10.00	17.50	22.13	31.25	40.00	31.88	40.62	32.50	33.75	36.25	28.75	21.25	13.75	10.00	377.63
	9.00	11.88	19.37	25.44	33.75	36.88	32.19	40.62	32.19	36.88	33.75	25.44	19.37	11.88	9.00	377.64
	4.97	6.55	10.69	14.03	18.62	20.35	17.76	22.41	17.76	20.35	18.62	14.03	10.69	6.55	4.97	208.35
3500	10.00	16.25	26.25	35.00	45.00	55.63	44.37	56.25	44.37	48.13	50.62	40.00	30.00	18.75	13.75	534.37
	11.88	17.50	28.12	37.50	47.81	51.88	44.37	56.25	44.37	51.88	47.81	37.50	28.12	17.50	11.88	534.37
	6.48	9.55	15.35	20.47	26.10	28.30	24.22	30.70	24.22	28.30	26.10	20.47	15.35	9.55	6.48	291.64

TABLE VIII—*Continued*

Load on tile, per linear ft.	Strips as Numbered															
	½	1	1½	2	2½	3	3½	4	4½	5	5½	6	6½	7	7½	Totals
	Bedding No. 2(d) Slightly Compacted Sand															
1680	2.50	3.37	4.63	9.75	29.37	23.12	43.13	41.75	43.12	33.13	12.50	9.13	4.12	0.50	0.12	260.24
	1.31	1.94	4.37	9.44	20.93	28.12	43.13	41.75	43.13	28.12	20.93	9.44	4.37	1.94	1.31	260.23
	0.70	1.04	2.35	5.08	11.26	15.13	23.20	22.46	23.20	15.13	11.26	5.08	2.35	1.04	0.70	139.98
2500	4.00	6.25	7.88	14.37	45.00	34.37	56.88	51.88	58.75	51.88	24.37	17.50	10.50	2.13	0.62	386.38
	2.31	4.19	9.19	15.94	34.69	43.13	57.81	51.88	57.81	43.13	34.69	15.94	9.19	4.19	2.31	386.40
	1.25	2.26	4.95	8.59	18.70	23.25	31.17	27.97	31.17	23.25	18.70	8.59	4.95	2.26	1.25	208.31
3500	7.00	11.25	13.75	26.25	63.13	45.00	67.50	61.88	72.50	72.50	45.00	33.13	21.25	5.50	2.00	547.64
	4.50	8.37	17.50	29.69	54.07	58.75	70.00	61.88	70.00	58.75	54.07	29.69	17.50	8.37	4.50	547.64
	2.40	4.46	9.32	15.81	28.80	31.29	37.28	32.96	37.28	31.29	28.80	15.81	9.32	4.46	2.40	291.68
	Bedding No. 3(d) Thoroly Compacted Sand															
1680	0.50	1.75	5.25	17.50	22.50	25.00	39.37	42.50	45.00	21.25	15.00	17.50	8.00	1.37	0.63	263.12
	0.56	1.56	6.62	17.50	18.75	23.13	42.18	42.50	42.18	23.13	18.75	17.50	6.62	1.56	0.56	263.10
	0.30	0.83	3.52	9.31	9.98	12.31	22.45	22.61	22.45	12.31	9.98	9.31	3.52	0.83	0.30	140.01
2500	1.62	3.25	8.13	30.00	33.75	39.37	55.00	57.50	63.75	35.63	24.37	26.25	11.25	2.25	1.37	393.49
	1.49	2.75	9.69	28.13	29.06	37.50	59.37	57.50	59.37	37.50	29.06	28.13	9.69	2.75	1.49	393.48
	0.79	1.46	5.13	14.89	15.39	19.85	31.43	30.44	31.43	19.85	15.39	14.89	5.13	1.46	0.79	208.32
3500	3.25	5.50	13.75	43.75	50.00	59.37	69.37	71.25	78.75	55.00	38.75	38.75	17.50	4.12	2.50	551.61
	2.87	4.81	15.62	41.25	44.37	57.19	74.06	71.25	74.06	57.19	44.37	41.25	15.62	4.81	2.87	551.59
	1.52	2.54	8.26	21.81	23.46	30.24	39.16	37.67	39.16	30.24	23.46	21.81	8.26	2.54	1.52	291.65

TABLE IX

Distribution of Pressure in the Upper Sand Bearing of a 22-Inch Tile Under Loads of 1680, 2500, and 3500 Pounds per Linear Foot

Under each loading the first line is the average pull of two independent sets of readings, the second line is the average of corresponding readings on the two sides of the center strip, while the data in the third line are those of line 2 reduced to loads on sections, corresponding to respective strips, per linear inch of tile. Each section, therefore, measures 1 by 1 1/16 inches

Load on tile, per linear ft.	Strips as Numbered															
	½	1	1½	2	2½	3	3½	4	4½	5	5½	6	6½	7	7½	Totals
	Room Dry Sand (0.05 per Cent Moisture)															
lb. 1680	10.63	10.00	11.25	12.50	20.00	21.88	21.88	29.38	23.75	21.88	15.00	10.63	10.00	10.00	11.87	240.65
	11.25	10.00	10.62	11.56	17.50	21.88	22.82	29.38	22.82	21.88	17.50	11.56	10.62	10.00	11.25	240.64
	6.55	5.82	6.18	6.73	10.18	12.73	13.28	17.09	13.28	12.73	10.18	6.73	6.18	5.82	6.55	140.03
2500	15.63	13.75	15.63	20.00	30.62	33.13	31.88	47.50	38.12	34.38	22.50	16.25	14.37	13.13	15.63	362.52
	15.63	13.44	15.00	18.12	26.56	33.75	35.00	47.50	35.00	33.75	26.56	18.12	15.00	13.44	15.63	362.50
	8.98	7.72	8.62	10.41	15.26	19.40	20.11	27.30	20.11	19.40	15.26	10.41	8.62	7.72	8.98	208.30
3500	20.00	18.75	20.00	26.88	42.50	46.88	46.88	66.87	55.63	47.50	31.87	23.13	16.88	15.63	19.37	498.77
	19.68	17.19	18.44	25.00	37.18	47.19	51.25	66.87	51.25	47.19	37.18	25.00	18.44	17.19	19.68	498.73
	11.51	10.05	10.78	14.62	21.74	27.60	29.97	39.11	29.97	27.60	21.74	14.62	10.78	10.05	11.51	291.65
	Sand Containing 5.0 per Cent Moisture															
1680	16.25	8.75	9.37	13.13	16.88	20.62	24.37	26.25	24.37	21.25	15.63	10.00	8.75	10.63	13.37	239.62
	14.81	9.69	9.06	11.56	16.25	20.94	24.37	26.25	24.37	20.94	16.25	11.56	9.06	9.69	14.81	239.61
	8.65	5.66	5.29	6.75	9.49	12.23	14.24	15.34	14.24	12.23	9.49	6.75	5.29	5.66	8.65	139.96
2500	22.50	11.68	11.68	20.62	28.13	32.50	35.63	40.63	37.50	32.50	21.25	18.75	12.50	15.00	20.00	360.87
	21.25	13.34	12.09	19.68	24.69	32.50	36.56	40.63	36.56	32.50	24.69	19.68	12.09	13.34	21.25	360.85
	12.27	7.70	6.98	11.36	14.25	18.76	21.11	23.46	21.11	18.76	14.25	11.36	6.98	7.70	12.27	208.32
3500	26.25	15.63	15.63	30.00	38.75	48.13	50.00	59.37	53.13	49.37	30.63	26.88	16.88	17.50	25.00	503.15
	25.62	16.57	16.25	28.44	34.69	48.75	51.56	59.37	51.56	48.75	34.69	28.44	16.25	16.57	25.62	503.13
	14.85	9.61	9.42	16.49	20.11	28.26	29.89	34.42	29.89	28.26	20.11	16.49	9.42	9.61	14.85	291.68

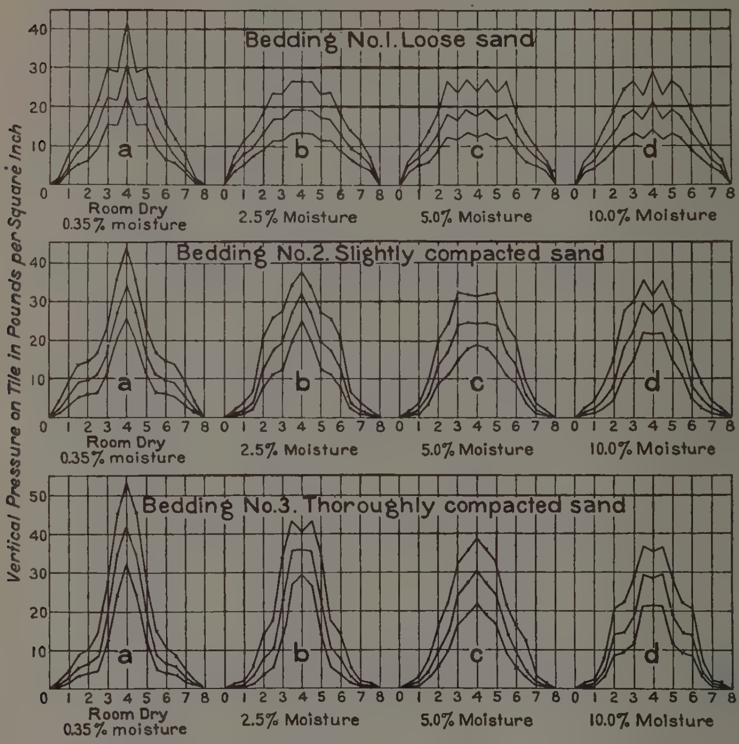


Fig. 26. Effect of Variation of Moisture Content of Sand and Compactness upon the Distribution of Pressure in the Lower Sand Bearing of a 22-Inch Tile Under Loads of 1680, 2500, and 3500 Pounds per Linear Foot

Some of the significant points developed by these studies, with friction strips, of bedding conditions are as follows:

1. For each of the three beddings, dry sand is the least satisfactory, as in all cases the concentration of loading has been greatest with dry sand.

2. The quantity of moisture in moist sand seems not to be of great importance altho perhaps the most consistent results were obtained with a moisture content of 5 per cent.

3. Loose sand is preferable to any degree of compactness, altho in no case is the pressure distribution uniform.

4. Pressure distribution in the top bearing of the A.S.T.M. standard sand bearing, while not uniform, is more nearly so under most conditions than in the bottom bearing.

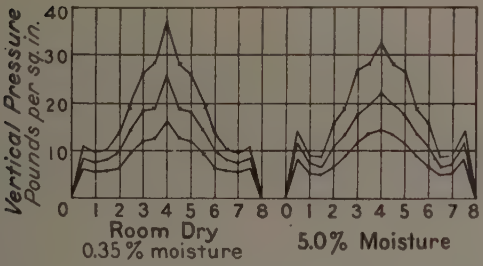


Fig. 27.. Effect of Variation of Moisture Content of Sand upon the Distribution of Pressure in the Upper Sand Bearing of a 22-Inch Tile Under Loads of 1680, 2500, and 3500 Pounds per Linear Foot

MATHEMATICAL SOLUTIONS OF STRESSES IN PIPE UNDER LOADINGS MEASURED BY FRICTION STRIPS

Figure 28 is a half-section of the center of wall of pipe being tested. Loads are assumed concentrated at center of wall thickness and center of strips as well. Loads are applied at points ½, 1½, etc. to 7½ at the center of each strip as shown in Figures 25 and 28. Right end (upper bearing) is assumed free; X_a being the unknown moment and X_b the unknown normal component to be found. We may proceed by summation from D to C, thence by integration from C to B, and again by summation from B to A.

Table X gives values of ds for each section and method of calculation.

TABLE X

VALUES OF DS

Section (upper bearing)	Sin ∝	∝	∝ (radians)	arc = ds	Section (lower bearing)
4	.08854	5° 5′	.08872	1.065	4
3½	.17708	10° 12′	.17802	1.072	3½
3	.26562	15° 24′	.26878	1.089	3
2½	.35417	20° 44.5′	.36211	1.119	2½
2	.44271	26° 17′	.45873	1.159	2
1½	.53125	32° 05′	.55996	1.216	1½
1	.61979	38° 18′	.66847	1.302	1
½	.70833	45° 06′	.78715	1.424	½

Table XI gives horizontal projections of midpoints of section from right end.

Table XII gives $\Sigma M'ds$ for upper bearing, dry sand, using 3500 pounds total load and considering 1 inch length of pipe for convenience in calculation. Column P gives the concentrated loads taken from Table VIII. Column M' (moments at midsection) is arrived at by taking 1, 3, 5, 7, etc., multiples of preceding values of P respectively;

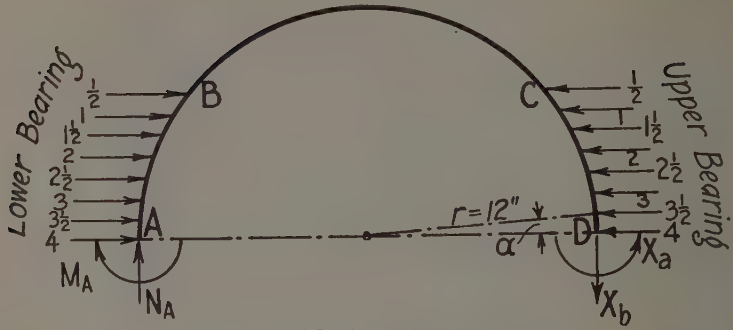


Fig. 28. Actual Loads on Pipe—Sand Bearing

$\frac{1.0625}{2}$, the length of one half-section, being omitted as a common multiple of all values of M′ while ds is taken from Table X.

TABLE XI

Horizontal Projection, Mid Point of Sections

Section	Sin α	α	Vers α	Horiz. proj. from right end ($\overline{x}$)
		Upper Bearing		
4	.04427	2° 32′	.00098	.0118
3½	.13281	7° 38′	.00886	.1063
3	.22135	12° 47′	.02481	.2977
2½	.30990	18° 3′	.04923	.5908
2	.39844	23° 29′	.08284	.9941
1½	.48698	29° 8′	.12657	1.5188
1	.57552	35° 8′	.18221	2.1865
½	.66406	41° 37′	.25233	3.0280
		Lower Bearing		
½				20.9720
1				21.8135
1½				22.4812
2				23.0059
2½				23.4092
3				23.7023
3½				23.8937
4				23.9882

The next step required the integration of M′ds from C to B and for this the resultant of forces acting on half the upper bearing is found.

Table XIII is that part of $\sum_{A}^{B}$ M′ds which is due to the resultant force on the upper bearing. Since 145.83 (the resultant force on 1 inch length of upper bearing) would be a common factor of all the terms of this summation, it can be temporarily omitted. The summation would then consist solely of values of ds multiplied by their respective lever arms, and the result would then be multiplied by 145.83

to obtain $\sum_{B}^{A} M'ds$.

Table XIV is the remainder of $\sum_{A}^{B} M'ds$, and is due to forces acting on lower quadrant. This is obtained in a manner analogous to Table XII.

Table XV is for the purpose of obtaining $\sum_{C}^{D} M'\bar{x}\, ds$. M′ is taken from the last column of Table XII and $\bar{x}$ from Table XI.

TABLE XII

UPPER BEARING, DRY SAND, TOTAL LOAD 3500 POUNDS (TABLE IX AND FIG. 27) AND USING 1-INCH LENGTH OF TILE. $\Sigma M'ds$

Section	P	M′	ds	M′ds
4	19.56	19.56	1.065	21
3½	29.97	88.65	1.072	93
3	27.60	215.31	1.089	235
2½	21.74	391.31	1.119	438
2	14.62	603.67	1.159	700
1½	10.78	841.43	1.216	1022
1	10.05	1100.02	1.302	1432
½	11.51	1380.17	1.424	1966
	145.83			5907

Table XVI gives that part of $\sum_{A}^{B} M'\bar{x}\, ds$ due to resultant force on upper bearing; M′ being taken from the last column of Table XIII.

Table XVII gives the remainder of $\sum_{A}^{B} M'ds$, due to forces acting on lower bearing. The M′ column is taken from Table XIV.

The values of $EI\delta_{aa}$ etc., have been developed under the previous analysis of the Minnesota bearing and need not be repeated here. Equa- analysis of the Minnesota bearing and need not be repeated here. Equation (34) is $-\delta'_a = X_a\ \delta_{aa} + X_b\ \delta_{ab}$ and Eq. (35) is $-\delta'_b = X_a\ \delta_{ba} + X_b\ \delta_{bb}$; the derivation of these equations having been previously explained. (See p. 27.) Solving, we get the value of $X_a = 758.6$; this being the moment in inch-pounds for one-inch length of pipe, at the top. Let $M = KPr$, where P is total load on pipe, and r is radius of middle of wall; K being an undetermined coefficient, then $758.6 \times 12 = M$; $P = 3500$ and $r = 12$. Solving for K we get

$$K = \frac{M}{Pr} = \frac{758.6 \times 12}{3500 \times 12} = .217 \qquad (36)$$

By solving X_b and taking moments at A we can find M_A and also K at point A.

In a similar manner, the values of K for the case where the lower bearing is type 1(c) are obtained; the only changes necessary being in Tables XIV and XVII, which are replaced by Tables XVIII and XIX.

For the Minnesota bearing (Fig. 4), the entire force exerted upon the upper bearing is concentrated at the top and we may evaluate its effect by a single integration from D to A and add to that the effect of the lower bearing already evaluated in Tables XIV, XVII, XVIII, and XIX.

$$\sum_{C}^{D} M'ds = 5907 \times \frac{1.0625}{2} = 3138$$

Resultant of above forces acts

$$\frac{(29.97 \times 1 + 27.60 \times 2 \text{ etc.})}{145.83} = 2.77'' \text{ above base.}$$

$$\int_{\pi/4}^{3\pi/4} M' r d\theta = \int_{\pi/4}^{3\pi/4} 145.83 \, (r \sin\theta - 2.77) \, r d\theta$$

$$= 12 \times 145.83 \int_{\pi/4}^{3\pi/4} (12 \sin\theta - 2.77) \, d\theta$$

$$= 1750 \left[- 12 \cos\theta - 2.77 \, \theta\right]_{\pi/4}^{3\pi/4} = 22084$$

TABLE XIII

BEDDING 3(a), DRY COMPACT SAND, TABLE VIII AND FIGURE 26

$\sum_{A}^{B}$ M'ds for Upper Bearing

Section	Lever arm	ds	Lever arm × ds +	Lever arm × ds −
½	5.20	1.424	7.405	
1	4.14	1.302	5.390	
1½	3.07	1.216	3.733	
2	2.01	1.159	2.330	
2½	.95	1.119	1.063	
3	−.11	1.089		.120
3½	−1.18	1.072		1.375
4	−2.24	1.065		2.386
			19.921	3.881
			− 3.881	
			16.040	

16.040 × 145.83 = 2339

TABLE XIV

Section	P	M′	ds	M′ds
½	1.94	1.94	1.302	2.5
1	5.00	10.82	1.216	13.2
1½	9.13	33.83	1.159	39.2
2	10.58	76.55	1.119	85.7
2½	15.27	145.12	1.089	158.0
3	28.11	257.07	1.072	275.6
3½	47.71	444.84	1.065	473.8
				1048.0

$$1048 \times \frac{1.0625}{2} = 557$$

$$EI\delta'_a = \Sigma M'ds = 3138 + 22084 + 2339 + 557 = 28118$$

$EI\delta'_b = \Sigma M'\bar{x}ds$ (where x = horizontal projection of mid point

$= \Sigma M'r \operatorname{vers}\theta \, rd\theta$ of section from right end.)

TABLE XV

UPPER BEARING

Section	M′	$\bar{x}$	M′$\bar{x}$
4	21	.0118	0
3½	93	.1063	10
3	235	.2977	70
2½	438	.5908	259
2	700	.9941	696
1½	1022	1.519	1552
1	1432	2.187	3132
½	1966	3.028	5953

$$11672 \times \frac{1.0625}{2} = 6201$$

TABLE XVI

LOWER BEARING

Section	M′	$\bar{x}$	M′$\bar{x}$ +	M′$\bar{x}$ −
½	7.405	20.972	155.3	
1	5.390	21.813	117.6	
1½	3.733	22.481	83.9	
2	2.330	23.006	53.6	
2½	1.063	23.409	24.9	
3	−.120	23.702		2.8
3½	−1.375	23.894		32.9
4	−2.386	23.988		57.2
			435.3	92.9
			− 92.9	
			342.4	

$$342.4 \times 145.83 = 49932$$

$$\int_{\pi/4}^{3\pi/4} 145.83\ (12\sin\theta - 2.77)\ (1 - \cos\theta)\ r^2 d\theta$$

$$= 145.83 \times 12^2 \int_{\pi/4}^{3\pi/4} (12\sin\theta - 2.77 - 12\sin\theta\cos\theta + 2.77\cos\theta)\ d\theta$$

$$= 42000 \left[12\sqrt{2} - \frac{2.77\pi}{2} \right] = 265007$$

TABLE XVII

Section	M′	$\bar{x}$	M′$\bar{x}$
½	0	20.972	0
1	2.5	21.813	55
1½	13.2	22.481	297
2	39.2	23.006	902
2½	85.7	23.409	2006
3	158.0	23.702	3745
3½	275.6	23.894	6585
4	473.8	23.988	11366
			24956

$$24956 \times \frac{1.0625}{2} = 13258$$

$$EI\delta_b' = 6201 + 265007 + 49932 + 13258 = 334{,}398$$

$$EI\delta_{aa} = \pi r = 37.70 \qquad EI\delta_{ab} = EI\delta_{ba} = \pi r^2 = 452.4$$

$$EI\delta_{bb} = \frac{3\pi r^3}{2} = 8143$$

$$28118 = 37.7\ X_a + 452.4\ X_b \tag{34}$$

$$334527 = 452.4\ X_a + 8143\ X_b \tag{35}$$

$$506124 = 678.6\ X_a + 8143\ X_b \quad \left(\text{Eq. } 34 \times \frac{8143}{452.4}\right) \tag{35a}$$

$$171597 = 226.2\ X_a \quad \left(\text{Eq. } 35\text{a}—\text{Eq. } 35\right)$$

$$X_a = 758.6 \qquad K = \frac{758.6}{3500} = .217 \tag{36}$$

$$452.4\ X_b = 28118 - 37.7\ (758.6)$$

$$X_b = -\frac{481}{452.4} = -1.06 \tag{37}$$

$$M_A = 758.6 - 24\ (-1.06) + (145.83 \times 2.77) - (1.94 \times 7 + 5.00 \times 6 \text{ etc.})$$

$$= 758.6 + 25.4 + 403.9 - 281.3 = 906.6 \tag{38}$$

$$K = \frac{906.6}{3500} = .259 \tag{39}$$

TABLE XVIII

Upper Bearing, Dry Sand, Lower Bearing 1(c) Table VIII and Figure 26, Loose Sand Containing 5 per Cent Moisture

Section	P	M′	ds	M′ds
½	6.61	6.61	1.302	8.6
1	10.16	30.09	1.216	36.6
1½	14.06	77.59	1.159	89.9
2	19.65	158.90	1.119	177.8
2½	28.45	288.31	1.089	314.0
3	25.24	472.41	1.072	506.4
3½	28.79	708.54	1.065	754.6
4	.....	......	.....	.....
				1887.9

$$1887.9 \times \frac{1.0625}{2} = 1003$$

$$EI\delta'_a = 3138 + 22084 + 2339 + 1003 = 28564$$

Note: $EI\delta'_a$ is calculated from values in Tables XII, XIII, and XVIII.

TABLE XIX

Section	M′	$\bar{x}$	$M'\bar{x}$
½	.0	20.972	0
1	8.6	21.813	188
1½	36.6	22.481	823
2	89.9	23.006	2068
2½	177.8	23.409	4162
3	314.0	23.702	7442
3½	506.4	23.894	12100
4	754.6	23.988	18101
			44884

$$44884 \times \frac{1.0625}{2} = 23845$$

$$EI\delta'_b = 6201 + 265007 + 49932 + 23845 = 340114$$

Note: $EI\delta'_b$ is calculated from values in Tables XV, XVI, and XIX.

$$28564 = 37.70\,X_a + 452.4\,X_b$$

$$\underline{344985 = 452.4\,X_a + 8143\,X_b}$$

$$\underline{514152 = 678.6\,X_a + 8143\,X_b}$$

$$169167 = 226.2\,X_a$$

$$X_a = 747.9 \qquad K = \frac{747.9}{3500} = .214 \tag{40}$$

$$X_b = \frac{28564 - (747.9 \times 37.70)}{452.4} = +\frac{368}{452.4} = +.81 \tag{41}$$

$$M_A = 747.9 - 24\,(.81) + 403.9 - (6.61 \times 7, \text{etc.})$$

$$= 747.9 - 19.5 + 403.9 - 420.8 = 711.5 \tag{42}$$

$$K = \frac{711.5}{3500} = .203 \qquad (43)$$

Minnesota Bearing—Bedding 3(a), Table VIII and Figure 26

$$\int_0^{\pi/2} 145.83\,(r \sin\theta)\, r d\theta = 21000\, \left[-\cos\theta\right]_0^{\pi/2} = 42000$$

From Table XIV, 557 must be added or $EI\delta'_a = 42557$

$$\int_0^{\pi/2} 145.83\ (r \sin\theta)\ (1 - \cos\theta)\ r^2 d\theta = 252000 \int_0^{\pi/2}$$

$$(\sin\theta - \sin\theta \cos\theta)\ d\theta$$

$$= 252000 \left[-\cos\theta - \frac{\sin^2\theta}{2} \right]_0^{\pi/2} = 504000$$

From Table XVII, 13258 must be added or $EI\delta'_b = 517258$

$$42557 = 37.7\, X_a + 452.4\, X_b$$

$$\underline{517258 = 452.4\, X_a + 8143\, X_b}$$

$$\underline{766026 = 678.6\, X_a + 8143\, X_b}$$

$$248768 = 226.2\, X_a \text{ or } X_a = 1096 \qquad (44)$$

$$K = \frac{1096}{3500} = .313 \qquad (45)$$

$$X_b = \frac{42557 - 37.7 = 1096}{452.4} = +2.74$$

$$M_A = 1096 - 24(2.74) - 281.3 = 749 \qquad (46)$$

$$K = \frac{749}{3500} = .214 \qquad (47)$$

Bedding 1(c), Table VIII and Figure 26

$EI\delta'_a = 43003$ and $EI\delta'_b = 527845$

Note: $EI\delta'_a$ and $EI\delta'_b$ were calculated from values in Tables XVIII, XIX, and Minnesota Bearing — Lower Bearing 3(a).

$$43003 = 37.7\, X_a + 452.4\, X_b$$

$$\underline{527845 = 452.4\, X_a + 8143\, X_b}$$

$$\underline{774054 = 678.6\, X_a + 8143\, X_b}$$

$$246209 = 226.2\, X_a$$

$$X_a = 1088 \qquad (48)$$

$$K = .311 \qquad (49)$$

$$X_b = \frac{43003 - 37.7 \times 1088}{452.4} = +4.39$$

$$M_A = 1088 - 24\,(4.39) - 420.8 = 562 \qquad (50)$$

$$K = \frac{562}{3500} = .161 \qquad (51)$$

STRENGTH RATIOS OF DIFFERENT BEARINGS

The results obtained by these mathematical solutions of stresses in pipes, under the loadings measured by friction strips, may be readily correlated with the strength tests of Table II and Figure 5 if it is kept in mind that the breaking load, for any given pressure distribution, is in proportion to the moment M, while for different pressure distributions the breaking load is inversely proportional to the value of the coefficient K. Therefore the Sand/Minnesota bearing ratio (of breaking loads) is equal to $\frac{.313}{.214} = 1.46$ by comparing Figures 29(C) and 29(B) and is equal to $\frac{.311}{.259} = 1.20$ by comparing Figures 29(D) and 29(A). By the use of moist, loose sand in the lower bearing and dry sand in the upper bearing the ratio becomes $\frac{.311}{.214} = 1.45$ when Figures 29(D) and 29(B) are compared.

The bearing conditions considered are extremes, and a pressure distribution between these extremes more nearly represents the conditions under which the tile tests were made as recorded in Table II. As a matter of fact, the mean of 1.46 and 1.20 is 1.33, which is very closely in agreement with the experimental value of 1.31 for the strength ratios as shown in Figure 5, for tile sizes 14 to 30 inches inclusive.

It will be noted that with the Minnesota bearing the maximum moment comes under the top bearing and the value of this moment changes very slightly under the extreme bedding conditions considered, the actual change being $\frac{.313}{.311} = 1.006$, or less than 1 per cent. This indicates that extreme care in bedding the tile is not necessary for an accurate test with the Minnesota bearing. With the sand bearing, under extreme bottom bedding conditions, shown in (A) and (B) of Fig. 29, the moment varies from a maximum at the bottom in one case to a maximum at the top in the second case, the actual difference being $\frac{.259}{.214} = 1.210$, or 21 per cent. It is evident from this that not only must some definite condition of bedding be specified, but also that extreme care must be used in bedding the tile if uniform test results are to be obtained with the sand bearings. As a consequence, it appears that the

Minnesota bearing is more suitable for routine tile testing than is the standard sand bearing.

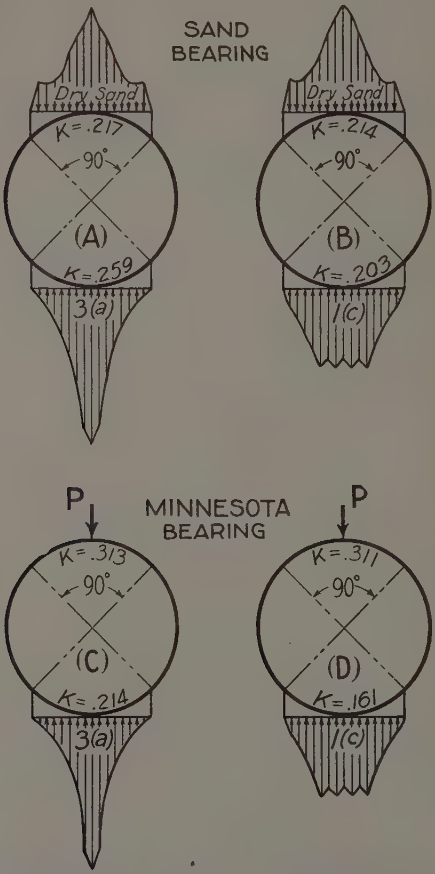


Fig. 29. Values of the Coefficient K, as Developed Mathematically, for Calculating, by the Equation $M = KPr$, the Moments for Load Distributions as Shown at Top and Bottom of Circular Pipe

For the same external load P, the moments at the uppermost point of tile in the three-edge bearings, as indicated by Equation (16), is very nearly the same as for tile in the Minnesota bearings, as indicated by Equations (45) and (49). At first thought this appears inconsistent in view of the different load-supporting strengths, as determined experimentally and illustrated in Figure 5, but can, at least in part, be accounted for as follows: (1) The moment due to own weight of tile differs greatly for the two bearings as it is 0.2385 Wr (27) for the two-edge bearing and 0.0707 Wr (28) for the Minnesota bearing, assuming parabolic distribution of pressure. Thus tile in the three-edge bearing start the test under handicap and consequently break under a smaller superimposed bending moment. This weight is negligible for small tile but becomes large for large tile. This is no doubt one factor that caused the apparent tendency of the sand/Minnesota ratio to decrease with the size of tile, as evidenced by Figure 5. In the main body of these tests there is some doubt as to the proper value of moment caused by own weight of tile, because the distribution of pressure had not been analyzed at the time the tests were made. There is, as a consequence, no way to correct the data for moment due to own weight. Such a correction applied to the 22-inch tile explains part of this discrepancy, but not all of it. (2) Another difference, and one which can not be quantitatively evaluated, is that for tile tested in the three-edge bearing the moment may reach its maximum almost simultaneously at each extremity of the vertical diameter while in the Minnesota bearing the moment always reaches its maximum in the upper extremity of the vertical diameter. Thus there are two chances for a weak spot to occur at a point of maximum moment in the three-edge bearing against one such chance in the Minnesota bearing. This means that the general average supporting strength for a number of tile tested in the three-edge bearing would be somewhat less than for the same tile tested in the Minnesota bearing. This, taken in connection with the additional moment produced by own weight of tile, probably explains the difference between the experimental data and the mathematical analyses as presented in this paper.

LOADS ON PIPES IN TRENCHES

Consideration of actual load requirements of pipes in trenches is closely related to the practical phase of tile testing. The nomograph of Figure 30 is presented to make available a simple means of readily determining the generally accepted load requirements, as determined experimentally by the Iowa State College of Agriculture and Mechanic Arts [10] [18] for three types of saturated soil most commonly encountered. Loads obtained by the use of scales (1) and (2) will closely agree with those given in Table II of the A.S.T.M. See Standard Specifications for Drain Tile.[6] This nomograph has been constructed from values derived by solution of the Marston [10] Formula $W = CwB^2$ in which

W = total weight on pipe, per unit of length.
w = weight of ditch filling, per unit of volume.
B = the breadth of the ditch a little below the top of pipe.
C = coefficient of loads on pipes in ditches and is the average vertical pressure per unit area in a ditch of unit width under a ditch filling material weighing unity per unit volume.

---

[6] Page 202, 1927 Book of A.S.T.M. Standards.

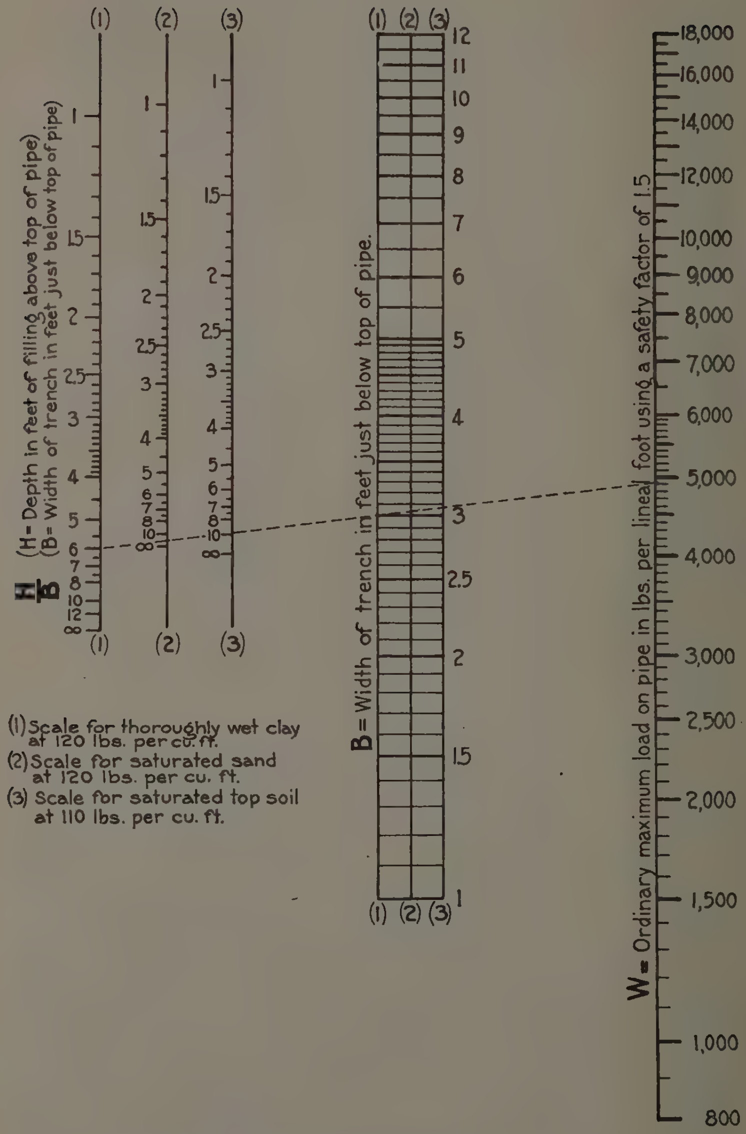


Fig. 30. Solution by Nomograph of Marston Formula for Calculating Loads on Pipes in Trenches

SUMMARY

1. From the experimental data of this report, the ordinary supporting strength of drain tile of diameters 6 to 30 inches tested in the three-edge bearing should be multiplied by the factor of 1.49 to reduce the test results to sand-bearing values. This checks almost exactly the 1.50 value recommended for drain tile by Committee C-6 of the A.S.T.M.

2. From the experimental data of this report, the ordinary supporting strength of drain tile of diameters 14 to 30 inches tested in the Minnesota bearing should be multiplied by the factor 1.31 to reduce the test results to sand-bearing values. In even figures this is a strength ratio of 4/3.

3. Summarizing the results of the mathematical analyses presented in this report on the basis of uniform distribution of pressure in the sand of both sand and Minnesota bearings, and assuming that the solutions of the equation for the two-edge bearing closely approximate conditions of the three-edge bearing, the theoretical strength ratio for the sand and three-edge bearings is $\frac{.3183}{.1687} = 1.89$, while that for the sand and Minnesota bearings is $\frac{.3054}{.1687} = 1.81$. As will be noted, neither of these values closely checks the experimental results.

4. Results of the mathematical analyses, as presented on the basis of parabolic distribution of pressure in the sand for both sand and Minnesota bearings, give a strength ratio for the sand and three-edge bearings of $\frac{.3183}{.2020} = 1.58$, and for the sand and Minnesota bearings $\frac{.3105}{.2020} = 1.54$. These values are still far from satisfactory, altho more closely in agreement with the experimental results than the values of paragraph 3.

5. Results of the mathematical analyses based on a pressure distribution in both sand and Minnesota bearings most unfavorable to the tile, as determined experimentally by the use of friction strips as recorded under Bedding 3(a) of Table VIII and illustrated in Bedding 3(a) of Figure 29, give a strength ratio for the sand and three-edge bearings of $\frac{.3183}{.259} = 1.23$, and for the sand and Minnesota bearings $\frac{.313}{.259} = 1.21$.

6. Results of the mathematical analyses based on the pressure distribution in both sand and Minnesota bearings most favorable to the tile, as recorded under Bedding 1(c) of Table VIII, and illustrated in Bedding 1(c) of Figure 29, give a strength ratio for the sand and

three-edge bearings of $\frac{.3183}{.214} = 1.49$, and for the sand and Minnesota bearings $\frac{.311}{.214} = 1.45$.

7. If the most unfavorable condition of bedding for the sand bearing be compared with the most favorable condition for the Minnesota bearing, the ratio is $\frac{.311}{.259} = 1.20$.

8. If the most favorable condition of bedding for the sand bearing be compared with the most unfavorable condition for the Minnesota bearing, the strength ratio is $\frac{.313}{.214} = 1.46$.

9. Taking the mean of the extreme values of the strength ratio of the sand and three-edge bearings as given in paragraphs 5 and 6, we have $\frac{1.23 + 1.49}{2} = 1.36$, which is considerably under the value of 1.49 as determined experimentally.

10. Taking the mean of the extreme values of the strength ratio of the sand and Minnesota bearings, as given in paragraphs 7 and 8, we have $\frac{1.20 + 1.46}{2} = 1.33$, which is in close agreement with the value of 1.31 as determined experimentally for tile sizes of diameters 14 to 30 inches, so that the factor of 4/3 for converting test results made with the Minnesota bearing to sand-bearing results appears reasonably accurate.

11. Except under most favorable conditions the concentration of loading on the bottom quadrant of pipe tested in the sand bearings is somewhat greater than generally assumed, while under unfavorable conditions it may be very much greater. Bedding with loose sand containing 2.5 and 5 per cent of moisture produces the most favorable conditions, in the matter of pressure distribution, while bedding with thoroly compacted dry sand produces the most severe. Considering all degrees of compactness of sand used in the tests, that with 5 per cent moisture gives the most consistent results.

12. The maximum moment for pipe tested in the sand bearing may be either at the top of the pipe or at the bottom, depending upon conditions of bedding.

CONCLUSIONS

A multiplying factor of 3/2, as generally used to reduce crushing strength tests of circular pipe made in the three-edge bearing to results on a sand-bearing basis, is closely correct.

A multiplying factor of 4/3 to reduce crushing strength tests of circular pipe made in the suggested Minnesota bearing to results on a sand-bearing basis is closely correct.

It is recommended, when applying the crushing test in the A.S.T.M. standard sand bearing, or in the suggested Minnesota bearing, that the sand used contain about 5 per cent moisture, and that the sand of the lower bearing be loosened by spading immediately before placing each tile for the test. Unless due attention be given both these details, consistent test results will not be obtained in the standard sand bearing.

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Owatonna Pipe and Tile Company, Owatonna
Quality Cement Products Company, Medford

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Agricultural Experiment Station

Regional and Seasonal Distribution of Moisture, Carbohydrates, Nitrogen, and Ash in 2-3 Year Portions of Apple Twigs

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CONTENTS

Page
Acknowledgments 6
Introduction 7
Materials and methods 8
  Collection and preparation of materials 9
  Preservation of material 10
  Methods of analysis 11
  Carbohydrate analyses 12
  Nitrogen analyses 13
  Ash analyses 13
  Tables and graphs 13
Variation in relative proportions of complex tissues 13
Regional and seasonal distribution of moisture 16
  Previous work 16
  General tendencies 17
  Growing period—April to September 20
  Transition between growing and dormant periods 21
  Dormant season—October to April 21
  Transition between dormant and growing periods 26
Regional and seasonal distribution of carbohydrates 26
  Total carbohydrates 30
  Pentosans 37
  Acid-hydrolyzable hexosans and sugars 39
    Sugars: growing period—April to September 39
    Acid-hydrolyzable hexosans: growing period—April to September ... 39
    Acid-hydrolyzable hexosan-sugar transformation: dormant period—September to March 40
    Causal mechanism 40
    Extent of acid-hydrolyzable hexosan disappearance 41
Regional and seasonal distribution of nitrogen 45
  Total organic nitrogen 45
  Amino and non-amino nitrogen 48
Regional and seasonal distribution of ash 50
  Dormant season 52
  Migration of mineral constituents from stem to shoots and leaves 52
Practical applications 53
  Analysis of plant organs 53
  Nutrition 53
  Winter hardiness 55
  Translocation 56
Conclusions 59
  Methods 59
  Moisture 59
  Carbohydrates 60
  Nitrogen 61
  Ash 62
Summary 62
Literature cited 63

ILLUSTRATIONS

Page

Fig. 1. Two 11-year-old "University" apple trees at beginning of experiment 8

2. The two apple trees toward the end of the experiment.............. 9

3. Method of separating complex tissues........................... 11

4. Seasonal variation in relative proportion of periderm. cortex-phloem, outer xylem, inner xylem-pith, periderm plus cortex-phloem, and outer xylem plus inner xylem-pith.......................... 15

5. Upper, seasonal distribution of moisture in periderm, cortex-phloem, outer xylem, inner xylem-pith, and entire twig; lower, precipitation from March 1, 1925 to Feb. 28, 1926.................. 18

6. Seasonal distribution of carbohydrates in periderm; acid-hydrolyzable hexosans; non-reducing sugars; reducing sugars; total sugars; pentosans; acid-hydrolyzable alcohol-insoluble carbohydrates; and total carbohydrates except cellulose....................... 27

7. Seasonal distribution of carbohydrates in cortex-phloem; acid-hydrolyzable hexosans; non-reducing sugars; reducing sugars; total sugars; pentosans; acid-hydrolyzable alcohol-insoluble carbohydrates; and total carbohydrates except cellulose........... 31

8. Seasonal distribution of carbohydrates in outer xylem; acid-hydrolyzable hexosans; non-reducing sugars; reducing sugars; total sugars; pentosans; acid-hydrolyzable alcohol-insoluble carbohydrates; and total carbohydrates except cellulose......... 32

9. Seasonal distribution of carbohydrates in inner xylem-pith; acid-hyrolyzable hexosans; non-reducing sugars; reducing sugars; total sugars; pentosans; acid-hydrolyzable alcohol-insoluble carbohydrates; and total carbohydrates except cellulose........ 33

10. Seasonal distribution of carbohydrates in the entire 2-3 year portion of the twig; acid-hydrolyzable hexosans; non-reducing sugars; reducing sugars; total sugars; pentosans; acid-hydrolyzable alcohol-insoluble carbohydrates; and total carbohydrates except cellulose 35

11. Lower, seasonal distribution of acid-hydrolyzable hexosans in periderm, cortex-phloem, outer xylem, and inner xylem-pith; upper, mean monthly minimum temperature......................... 36

12. Seasonal distribution of acid-hydrolyzable hexosans; total sugars, and pentosans in periderm, cortex-phloem, and entire twig.......... 37

13. Seasonal distribution of acid-hydrolyzable hexosans; total sugars, and pentosans in outer xylem, inner xylem-pith, and entire twig.... 38

14. Lower, seasonal distribution of total organic nitrogen in periderm, cortex-phloem, outer xylem, inner xylem-pith, and entire twig; upper, amino and non-amino nitrogen in the same complex tissues and the entire twig.. 46

15. Seasonal distribution of amino nitrogen in periderm, cortex-phloem, outer xylem, and inner xylem-pith.......................... 49

Page

16. Lower, seasonal and regional distribution of ash in periderm, cortex-phloem, outer xylem, inner xylem-pith, and entire twig; upper, seasonal and regional distribution of total carbohydrates (except cellulose) in the four complex tissues—periderm, cortex-phloem, outer xylem, and inner xylem-pith 51
17. Carbohydrate-nitrogen ratios; entire twig; total sugar-nitrogen ratio; acid-hydrolyzable hexosan-nitrogen ratio; and total carbohydrate-nitrogen ratio 54
18. Total sugar-nitrogen ratios; periderm, cortex-phloem, outer xylem, inner xylem-pith, and entire twig 56
19. Acid-hydrolyzable hexosan-nitrogen ratios; periderm, cortex-phloem, outer zylem, inner xylem-pith, and entire twig 57
20. Total carbohydrate-nitrogen ratios; periderm, cortex-phloem, outer xylem, inner xylem-pith, and entire twig 58

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REGIONAL AND SEASONAL DISTRIBUTION OF MOISTURE, CARBOHYDRATES, NITROGEN, AND ASH IN 2-3 YEAR PORTIONS OF APPLE TWIGS[1]

By Hamilton Paul Traub

INTRODUCTION

An understanding of the physiology of woody plants is of first importance to those engaged in the culture of trees and shrubs. Only by a clear conception of the functioning of the tissues of the woody plant can any real progress be made toward the solution of such important problems as translocation of food, fruit-bud formation, and winter hardiness in trees. Anything that might add to the accumulating scientific knowledge of the physiology of the apple tree would serve as part of the foundation upon which the superstructure of cultural practices may be based. The experiments reported in this paper were undertaken in September, 1924, in the hope of making a slight contribution toward a clearer understanding of the functioning of the complex tissues of the apple tree. The main interest centers around a purely physiological problem; but any advance in the basic sciences usually finds immediate application in the related applied sciences.

In carrying out the research. the method of macrochemical analysis of the complex tissues of the 2-3 year portions of apple twigs was utilized in an attempt (1) to extend the researches in tree physiology initiated by Geleznow (1878), at St. Petersburg (Leningrad); and Craib (1918), at Edinburgh, on moisture relations; Alfred Fischer (1888, 1891), and Niklewski (1906), at Leipzig, on the starch-oil and starch-sugar transformations in woody plants, and (2) to study the distribution of nitrogen and mineral matter in the apple tree on the basis of complex tissues throughout the season.

The work is developed under the following heads: (1) Materials and methods, (2) variation in the relative proportions of the complex tissues, (3) regional and seasonal distribution of moisture, (4) regional and seasonal distribution of carbohydrates, (5) regional and seasonal distribution of nitrogen, (6) regional and seasonal distribution of ash, (7) practical application, (8) conclusions, and (9) summary.

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[1] Also submitted to the faculty of the Graduate School of the University of Minnesota in partial fulfilment of the requirements for the degree of Doctor of Philosophy. Degree granted June, 1927.

MATERIALS AND METHODS

This section is devoted to a more detailed description of the materials and methods employed in this research, which were briefly described by Traub (1927).

In order that results from one date to another should be comparable, special care was taken to obtain sufficient homogeneous material to carry through the experiment for at least two years. After considering other possibilities, including a plan of cutting down one 11-year-old apple tree for each sample, it was finally decided to limit the study to the 2-3 year portion of apple twigs. According to this plan, portions (of the dormant twig) in the second year of growth, in March, were taken as the first material for analysis. Similar portions of twigs were taken for analysis on selected dates from March (into the third year of growth) to February of the following year. With the adoption of this method it was possible to confine operations to a single or at most two trees of the same variety growing under similar conditions and with similar performance records, for the amount of material removed in any one year was not sufficient to change unduly the nutritive balance of the trees. This procedure made possible an intensive study of the complex tissues of one winter-hardy apple variety under the climatic conditions of central Minnesota. The results obtained should, therefore, be interpreted on this basis.

Fig. 1. Two 11-year-old "University" apple trees at the beginning of the experiment, September, 1924. Trees planted at University Farm, St. Paul, Minnesota, May 6, 1914.

Two 11-year-old "University" apple trees *(Pyrus malus)* were used for the experiment. This is a late fall, yellow-fruited seedling of Oldenburg originated and introduced by C. G. Patten, Charles City, Iowa, in 1882. The variety has been described by Hansen (1902) and Green (1903). The tree is an annual bearer; vigorous and quite winter hardy under central Minnesota conditions. The trees selected are located on the Agricultural campus, University of Minnesota, St. Paul. They were planted in May, 1914, in silt loam with a clay subsoil, and were in sod culture after the first few years of clean cultivation. The trees have always been vigorous and have similar performance records. Since they came into bearing, the trees have produced comparatively light crops of fruit annually. The condition of the trees at the beginning of the experiment, September, 1924, is portrayed in Figure 1. The same trees toward the end of the experiment, December, 1926, are shown in Figure 2. At this time the trunk diameter of the trees measured 6½ and 7 inches respectively; the height 16½ and 16¾ feet; and the spread 16 and 17 feet.

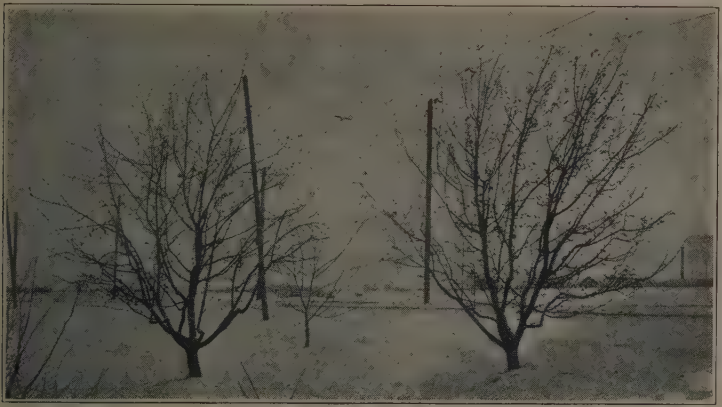

Fig. 2. The two "University" apple trees toward the end of the experiment, Dec. 11, 1926. Trunk diameter 6½ and 7 inches, height 16½ and 16¾ feet, and spread 16 and 17 feet.

Collection and Preparation of Materials

Samples were taken at twenty different times during the season, but not at regular intervals. During the periods April to May and September to October, when environmental changes bring about very pronounced physiological transformations, studies were more intensive than at other seasons of the year. All the samples were analyzed for total moisture and reducing and total sugars. With these facts as a basis, what appeared to be critical periods in the seasonal cycle were selected. The remaining material collected on these dates was used for additional determinations: acid-hydrolyzable alcohol-insoluble carbohydrates, pentosans, total and amino nitrogen, and ash.

About 125 grams of material were collected for each sample, always between the hours of 7:30 and 8:30 in the morning, within a range of several feet and about 8 feet from the ground from the north, south, east, and west sides of the trees. The material was brought to the laboratory in a vasculum and was quickly separated by means of a sharp grafting knife into the four fractions—periderm,[2] cortex-phloem, outer xylem, and inner xylem-pith, as indicated in Figure 3. A longitudinal incision was made in the twig with a sharp grafting knife, and the periderm was then peeled off as indicated in Figure 3. During most seasons of the year the periderm was fairly easily separated, but this operation was usually the most tedious part of the procedure as great care had to be exercised not to take parts of the cortex. The tissues between the periderm and xylem tissues, designated hereafter as cortex-phloem, were next scraped off as a second complex tissue, leaving the wood and the pith. The outer greenish-tinged xylem was stripped off as a third complex tissue by means of a sharp grafting knife, leaving the inner whitish and drier xylem-pith as a fourth complex tissue. The various complex tissues were kept in closed specimen jars after separation. The separated material in each case was cut into small pieces by means of pruning shears and the pieces were thoroly mixed. The fractions of each of the four complex tissues for the macrochemical analyses were then preserved.

Preservation of Material

For the quantitative macrochemical analyses the material representing each of the four complex tissues—periderm, cortex-phloem, outer xylem, and inner xylem-pith—was divided into two major fractions:

(a) Fractions for drying to be used for the determination of moisture, organic nitrogen, and ash.

(b) Fractions to be preserved in alcohol for the determination of reducing and total sugars, acid-hydrolyzable alcohol-insoluble carbohydrates, pentosans, and amino nitrogen.

The first major fractions were dried to constant weight at 102°C. for moisture determinations, and the residue was then ground in a drug mill to a fine powder to be used for the estimation of organic nitrogen and ash.

The second major fractions of the cortex-phloem, outer xylem, and inner xylem-pith were again divided into duplicate samples for analysis.

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[2] Eames, A. J. and MacDaniels, L. H. An introduction to plant anatomy. First ed., p. 213. New York. 1925. Confirmed by letter from A. J. Eames, Cornell Univ., Ithaca, N. Y., Dec. 8, 1926.

Because of the small quantity of periderm tissue, single samples were preserved.

The material was preserved by putting it immediately after the final mixing and weighing into Mason jars containing boiling 95 per cent alcohol to which 1 gram of calcium carbonate had been added. After boiling for 30 minutes, the jars were sealed and stored for analysis at a convenient time.

Methods of Analysis

The samples were extracted with alcohol in Landsiedl extractors over a steam bath for 24 hours. Previous experiments had shown that after 18 hours any further extraction was equivalent to a blank, even when the tissue was broken further.

The alcohol-insoluble residue remaining in the extraction cup was then dried to constant weight at 102°C. and ground in a drug mill to a fine powder to be used in the determination of total acid-hydrolyzable alcohol-insoluble carbohydrates (hexosans and pentosans), and pentosans. After making up to volume, the alcohol-soluble extract was treated with chloroform to separate the crude lipides (fats, lecithin, chlorophyll, etc.). The remaining alcohol-soluble phase was divided into

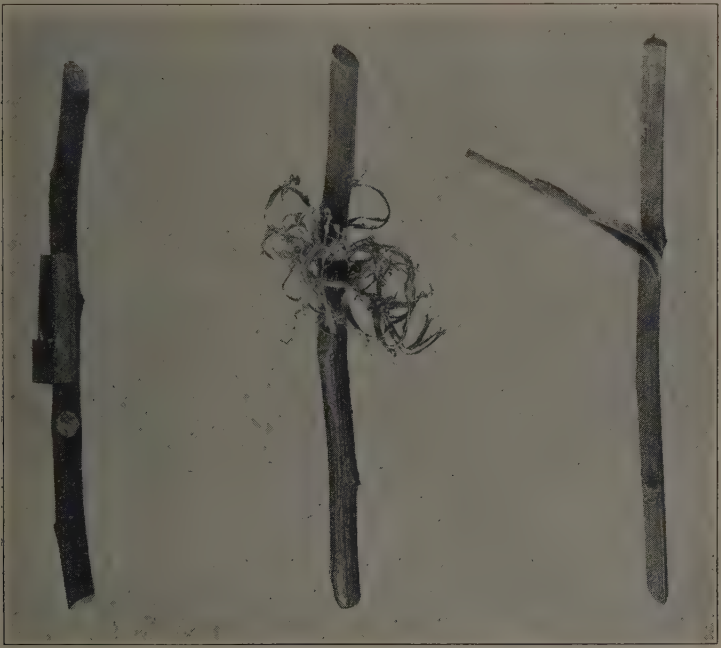

Fig. 3. Method of separating complex tissues—periderm, cortex-phloem, outer xylem, and inner xylem-pith.

aliquots for the determination of reducing sugars, total sugars, and amino nitrogen, the alcohol being removed in Claissen flasks under reduced pressure at a temperature of 40-60°C.

Duplicate samples were analyzed, except in the case of the periderm material, and all analyses were made in duplicate except those of the sugars, which were in triplicate.

The official methods of analysis of the Association of Official Agricultural Chemists (1925) were used throughout with a single slight modification as indicated under carbohydrate analyses.

Carbohydrate Analyses

In the determination of reducing and invert sugars according to the Munson and Walker method, the volumetric thiosulphate method of estimating precipitated cuprous oxide was used except that bromine water was omitted from the process.

In the estimation of total sugars, hydrolysis was accomplished by allowing 50 cc. of the clarified solution, to which 10 cc. of dilute hydrochloric acid (sp. gr. 1.1029) had been added, to stand 24 hours at a temperature of 20-24°C.

According to Harvey (1923, 1925), the presence of phloridzin in apple tissue may lead to serious errors in sugar determinations unless necessary precautions are taken in technical procedure. Harvey suggested, however, that the method of inversion at room temperature for 24 hours might avoid the hydrolysis of phloridzin. This was essentially the method of hydrolysis employed in all the sugar determinations, but it was considered advisable to check this point. For this purpose phloridzin was tested in saturated solution before and after hydrolysis at room temperature for 24 hours, by using 25-cc. portions for reduction with standard Fehlings solution. The results were equivalent to blank determinations in each case.

The method of direct acid hydrolysis was used in the determination of the acid-hydrolyzable alcohol-insoluble carbohydrates, i.e., acid-hydrolyzable material including starch. The results obtained by this method include the pentosans and other carbohydrate bodies that undergo hydrolysis and are converted into reducing sugars on boiling with hydrochloric acid. Two grams of dry material was stirred in a beaker with 50 cc. of cold water for an hour, transferred to a filter, and washed with 250 cc. of cold water. The insoluble residue was heated for 2½ hours with 200 cc. of water and 20 cc. of dilute hydrochloric acid (sp. gr. 1.125) in a flask provided with a reflux condenser. After cooling, nearly neutralizing with sodium hydroxide, completing volume to 250 cc., and filtering, the glucose was determined in aliquots of the filtrate.

Pentosans were determined by the phloroglucinol method. The quantity obtained was subtracted from that of the acid-hydrolyzable alcohol-insoluble carbohydrates, leaving the acid-hydrolyzable hexosans, including starch.

Nitrogen Analyses

Amino nitrogen was determined by the Van Slyke method. The mixture of glacial acetic acid, sodium nitrite, and the solution of the sample was shaken for 5 minutes.

The total organic nitrogen was determined according to the Gunning modification of the Kjeldahl method.

Ash Analyses

Total ash was determined by burning in a porcelain crucible 2 grams of the dry powdered residue from the moisture determinations for each analysis in a muffle oven until a white or grayish white residue was obtained.

Tables and Graphs

The complete analytical data are given in Tables I, II, and IV to XV inclusive. The results are shown graphically in Figures 4 to 20 inclusive.

VARIATION IN RELATIVE PROPORTIONS OF COMPLEX TISSUES

That the relative proportions of the complex tissues did not remain constant from one date to another under the conditions of the research, was determined in the preliminary experiments from September to December, 1924. This fact was also reported by Proebsting (1925), but he made no attempt to put it on a quantitative basis.

From a theoretical viewpoint, the difference in the relative proportions of the complex tissues at various seasons of the year may be due to (1) variation in the diameter of the twigs utilized, introducing varying volumes of the complex tissues, (2) variation in the dry weight without change in volume due to the translocation of substances into and out of a region, and (3) growth (increase in tissue) or senescence (decrease in tissue due to absorption after death) in a part of the complex tissues without a corresponding change in the remaining tissues. Further experimentation is necessary to establish the relative importance of these various sources of error when entire twigs are analyzed at various seasons of the year.

Errors due to variation in diameter of the twig can be minimized by selecting twigs as nearly alike in diameter as possible throughout the experiment. There seems to be no remedy for errors due to the normal seasonal physiological processes of the plant—translocation of material into and out of a region, and growth or senescence of tissues.

The seasonal variation in the relative proportions of the complex tissues throughout the experiment are indicated in Table I in per cent dry weight, and are shown graphically in Figure 4.

TABLE I

SEASONAL VARIATION IN RELATIVE PROPORTIONS OF PERIDERM, CORTEX-PHLOEM, OUTER XYLEM, AND INNER XYLEM-PITH, IN 2-3 YEAR PORTIONS OF APPLE TWIGS, MARCH 7, 1925, TO FEBRUARY 26, 1926

Expressed in per Cent of Total Dry Weight

Date	Periderm	Cortex-phloem	Outer xylem	Inner xylem-pith	Periderm plus cortex-phloem	Outer xylem plus inner xylem-pith
March 7	8.25	17.21	44.31	30.23	25.46	74.54
April 4	8.10	18.97	43.05	29.88	27.07	72.93
May 16	8.16	19.85	44.24	27.75	28.01	71.99
June 20	8.61	15.02	44.99	31.38	23.62	76.38
September 17..	4.37	17.75	44.26	33.62	22.12	77.88
October 10....	8.06	18.22	38.93	34.79	26.28	73.72
October 23....	3.10	16.68	46.98	33.24	19.78	80.22
December 23 ..	6.17	17.73	41.46	34.64	23.90	76.10
February 26 ..	7.66	18.78	41.56	32.00	26.44	73.56
Average ..	6.94	17.80	43.31	31.95	24.742	75.258

The data given in Table I show that on the basis of complex tissues—periderm, cortex-phloem, and outer xylem plus inner xylem-pith[3]—there are marked fluctuations in the relative proportions of these complex tissues. The variations are quite significant, amounting to 8.23 per cent on a dry weight basis in the periderm plus cortex-phloem and outer xylem plus inner xylem-pith.

Tables IV, V, and VIII show that in the spring the xylem tissues, composing over 70 per cent of the total dry weight, and functioning as winter storage organs, lose a relatively large part of their stored material by translocation, and the relative proportion of the cortex-phloem rises correspondingly. In late October this is reversed—a relatively large part of the reserve food is translocated and stored in the xylem tissues, and there is a corresponding decline in the relative proportions of periderm and cortex-phloem. Other factors may, however, be operative. Hanson (1926) has shown that in *Acer saccharinum* under eastern Nebraska conditions, xylem formation begins between April 20 and 27, when leaves are about half grown; production of new cells is very active throughout May and June, and by August 1 most of the xylem is formed and over 90 per cent is lignified. By August 15 lignification is complete to the cambium, and no new cells are being formed; by September 14 cambial activity is renewed, and new xylem is being developed, and by October 14 cell formation has ceased and the xylem is completely lignified. The abrupt variations in the relative proportions of the complex tissues in 2-3 year portions of apple twigs during April-May, and September-October, under central Minnesota conditions, may be connected with cambial activity. There is also the possibility that during periods of cambial activity, undifferentiated cells on the xylem side of the cambium may adhere to the cortex-phloem fraction during the separation, thus apparently increasing the relative portion of this tissue. However, the proportion of the phloem begins to rise in early March when the trees are dormant and before there is likely to be any cambial activity, indicating that the change is due apparently to translocation of material from the xylem tissues.

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[3] The outer xylem and inner xylem-pith are not considered separately, as it may be argued that an error might be introduced when separations are made.

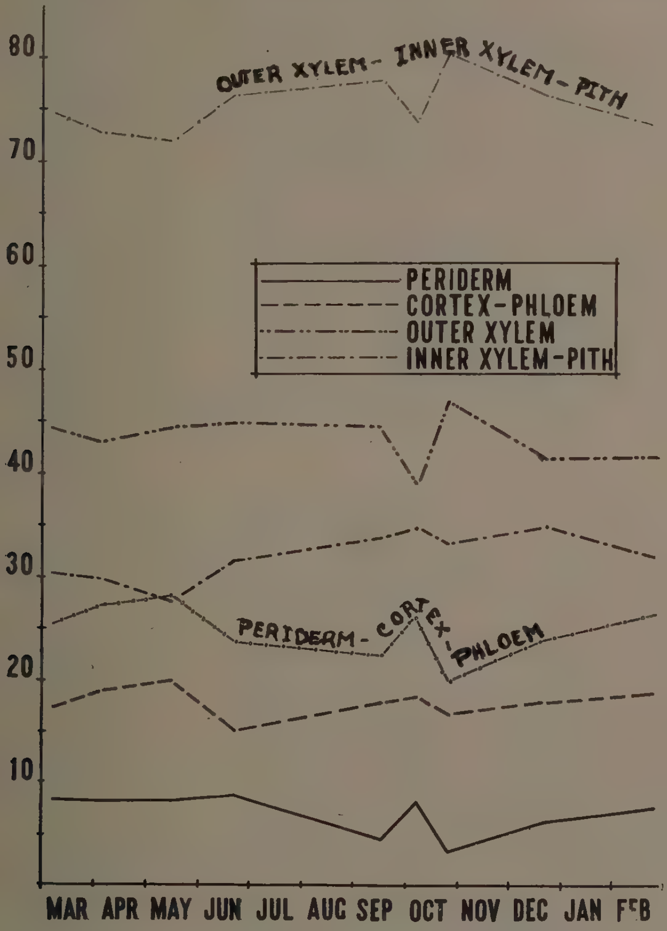

Fig. 4. Seasonal variation in the relative proportion of periderm, cortex-phloem, outer xylem, inner xylem-pith, periderm plus cortex-phloem, and outer xylem plus inner xylem-pith. Expressed in per cent dry weight.

In conclusion, the gross analysis of the plant organs (twigs, spurs, roots, etc.) in seasonal studies is on the defensive.[4] At least, the error that may be introduced by using this method should be fully recognized in the interpretation of data based upon the analysis of entire plant organs composed of complex tissues that may vary in their relative proportions from one date to another. The whole problem requires thoro investigation.

REGIONAL AND SEASONAL DISTRIBUTION OF MOISTURE

In the study here reported, an attempt was made to come a little closer to a quantitative estimation of the seasonal moisture relations of the complex tissues of 2-3 year portions of apple twigs—periderm, cortex-phloem, outer xylem, and inner xylem-pith. We are not concerned alone with such seasonal variation of total moisture content of the stem as reported, for instance, by du Sablon (1904, 1906) for the pear and other trees, but rather with an estimation of the individuality of the various complex tissues with respect to seasonal moisture distribution and its physiological significance.

Previous Work

Several workers have reported experiments on the subject of seasonal and regional variation of the moisture content in the stems of woody plants.

Geleznow (1876), at St. Petersburg (Leningrad), carried out experiments showing the seasonal distribution of moisture in the cortex-phloem and wood of *Acer platanoides, Betula alba, Populus tremula,* and *Pinus sylvestris.* He concluded that the cortex-phloem usually contains more moisture than the wood.

Craib (1918, 1920, 1923) reported experiments on the regional spread of moisture throughout the year in the trunk of *Acer pseudoplatanus,* and other trees. He showed that there are considerable seasonal fluctuations of moisture in the different portions of the wood: at the beginning of the leafless period, October, the center of the tree is very wet; at the end of the same period, March, there is a very wet region near the outside and the center is very dry; between these two extremes occur all the intermediate stages. During the leaf-bearing period, March to May, it appears probable that the moisture goes through the same movement on a reduced scale and at a greatly accelerated speed as in the longer interval, October to March. When the full-leaf stage is reached, throughout most of the tree the whole central area of the wood has an almost uniform percentage of moisture, and the youngest wood has a relatively high moisture content.

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[4] It may be argued that the same criticism that applies to the analysis of the plant organ made up of complex tissues would also apply, to a lesser extent, to the comparative study of complex tissues. This is true, but for practical reasons it will probably not be possible to separate the complex tissues into simple tissues for macrochemical analysis.

Immink (1923) reported experiments with teakwood and mahogany trees in which he claims to have obtained results similar to those reported by Craib with *Acer pseudoplatanus*.

Craib (1925)[5] suggested to the writer that Craib's results (1918) might be connected with the work of Templeton (1923) on starch distribution in the trunk of *Acer pseudoplatanus* at various heights above ground level. Templeton used the same series of trees and followed the same plan for the different level cuts and his results should, therefore, be comparable with those of Craib (1918).

General Tendencies

The researches reported above were concerned either with cortex-phloem and xylem or with xylem tissues alone. In this work the seasonal distribution of moisture has been followed in the four complex tissues—periderm, cortex-phloem, outer xylem, and inner xylem-pith. The results obtained are expressed as moisture in per cent dry weight in Table II, and are shown graphically in Figure 5.

TABLE II

REGIONAL AND SEASONAL DISTRIBUTION OF MOISTURE IN 2-3 YEAR PORTIONS OF APPLE TWIGS, MARCH 7, 1925, TO FEBRUARY 26, 1926

Expressed in per Cent Dry Weight

Date	Periderm	Cortex-phloem	Outer xylem	Inner xylem-pith	Whole twig
March 7	17.13	96.04	58.57	45.93	57.77
March 27	28.79	97.17	47.08	47.80	54.78
April 4	58.33	65.33	53.83	53.23	55.31
April 18	65.62	117.19	61.16	57.92	71.05
May 2	75.12	153.37	72.56	66.24	86.53
May 16	80.98	125.88	70.76	71.65	82.78
May 30	81.69	139,20	80.21	73.50	90.20
June 20	35.01	167.16	92.03	71.32	91.89
July 18	44.17	120.79	91.94	71.65	87.41
August 18	57.25	132.68	65.01	66.88	74.70
September 17	67.61	119.64	79.76	64.49	81.17
October 4	52.46	102.89	74.27	52.61	70.45
October 10	48.65	100.83	58.51	52.44	60.89
October 23	64.63	106.75	58.77	59.39	67.16
December 23	29.52	74.85	61.59	47.40	57.04
January 29	24.11	62.74	59.00	55.14	56.73
February 26	18.15	88.96	54.43	56.26	58.72

The results show wide variation in amount of moisture for the various tissues. During certain times of the year there is also a difference in trend in the periderm.

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[5] Letter from William G. Craib, Dept. of Botany, Univ. of Aberdeen, Old Aberdeen, Scotland, Dec. 6, 1925, to Hamilton P. Traub.

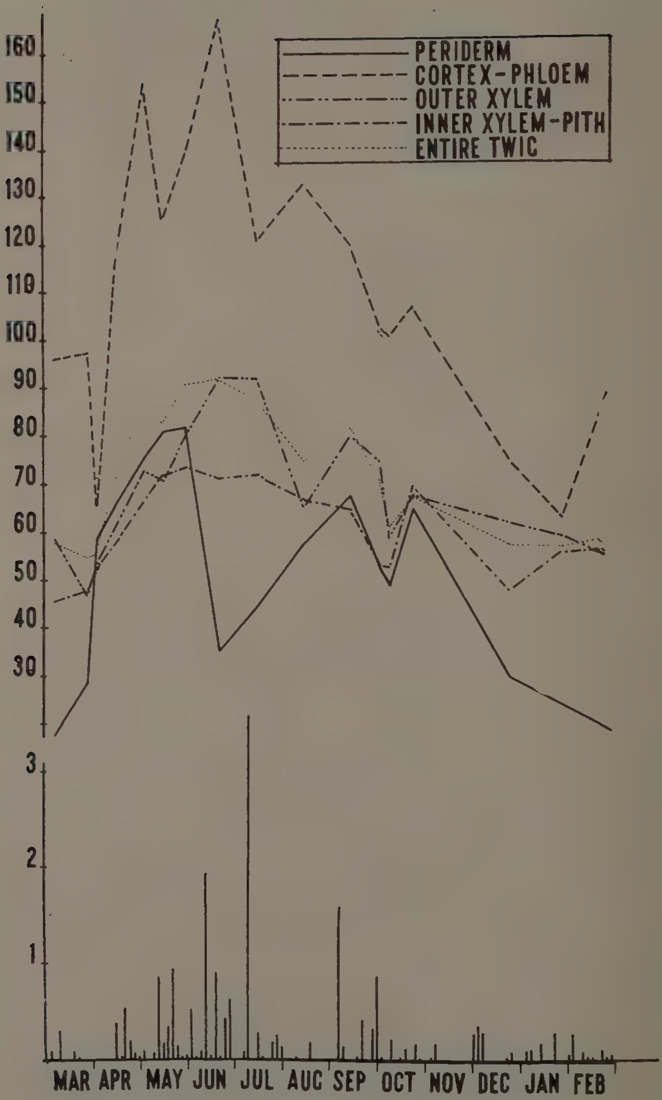

Fig. 5. Upper, seasonal distribution of moisture in periderm, cortex-phloem, outer xylem, inner xylem-pith, and entire twig. Expressed in per cent dry weight.

Lower, precipitation from March 1, 1925, to February 28, 1926, in three-day summation periods. Expressed in inches. From Annual Meteorological Summary, 1925 and 1926, U. S. Weather Bureau, Minneapolis, Minnesota, Station.

The highest percentage of moisture during the entire year is found in the cortex-phloem. Geleznow (1876) found a similar condition in *Acer* and other trees. The range in the cortex-phloem on a dry weight basis varies from 65.33 to 167.16 per cent, a difference of 101.83 per cent. The cortex-phloem contains a relatively greater proportion of living tissue than the xylem and a correspondingly greater moisture content would be expected. This is actually the case.

The two xylem tissues, outer xylem and inner xylem-pith, follow the same trend except that the per cent moisture in the outer xylem shows a tendency to run higher at practically all times of the year. This is especially marked during the summer. There is a range from 47.08 to 92.03 per cent, a difference of 44.95 per cent in the outer xylem; and a range from 47.80 to 73.50 per cent, a difference of 25.70 per cent, in the inner xylem-pith. There is, therefore, a significant and consistent lower moisture content in the xylem tissues than in the cortex-phloem.

The moisture content of the periderm is usually lower than that of the xylem tissues. There is a comparatively wide range, from 17.13 to 81.98 per cent, a difference of 64.85 per cent, but the absolute amount reaches above that of the xylem tissues for relatively short periods only. In the periderm, there is not only a difference in amount but also a difference in trend from the end of May to the middle of August. While the moisture in the cortex-phloem and outer xylem rises from the end of May to the end of June, the moisture in the periderm falls off; when the moisture falls in the cortex-phloem, from the end of June to the middle of July, and in the outer xylem from the end of June to the middle of August, the moisture rises in the periderm. After the middle of August the moisture content of the periderm has the same trend as in the other tissues, but it has a tendency to be lower than in the other tissues during the winter, with a temporary rise above the xylem tissues from early April until the end of May.

When the moisture data are calculated on the basis of the entire twig, the individuality of the complex tissues naturally disappears and the tendency of the tissue, outer xylem, in greatest relative abundance, is reflected. The range of moisture content, 54.78 to 91.89 per cent, a difference of 37.11 per cent, closely approaches that of the outer xylem. The error introduced by this method of expressing quantitative results has been emphasized above.

In the following discussion the moisture relations in the four complex tissues will be followed through the physiological periods—the growing period, the transition between growing and dormant periods, the dormant period, and the transition between dormant and growing periods.

Growing Period—April to September

In general, the summer maximum of moisture in all the complex tissues is reached, under central Minnesota conditions, between April 3 and September 14, when precipitation is greatest—over 70 per cent of the annual total.

The fluctuations in amount of moisture during the season are considerable in these four tissues. The rise in early April begins before much precipitation has fallen. The rains begin about the middle of April but the first maximum is not reached by all the tissues until May. There is a temporary decline in moisture content of the cortex-phloem and outer xylem, followed by another maximum in June for the cortex-phloem and from late June to the middle of July for the outer xylem. The summer minimum of the periderm is attained at this time. It seems strange that there should be an actual decline in moisture in the cortex-phloem during the month of heaviest rainfall, July, and an increase to a third maximum during the month of least rainfall, August. The decline of moisture content in periderm and cortex-phloem during periods of abundant rainfall points to the fact that when there is an optimum water supply the actual amount of water taken up is limited by vital phenomena and that under such conditions there is no direct proportionality between total rainfall and the amount of moisture in the individual complex tissues. The correlation between the total moisture in the twig and total rainfall, however, is much closer, following the trend of the outer xylem, which as an individual tissue shows the same relationship. The outer xylem apparently serves as a complex water-supplying tissue. The periderm and cortex-phloem seem to act independently of the total precipitation within the summer maximum, selecting varying amounts of water from the common supplying tissue with the changing chemical and physical state of the protoplasm.

The inner xylem-pith reaches a maximum moisture content by the middle of May and shows only very slight fluctuations, and a very gradual downward trend to the middle of September. The rapid decline in moisture content of the periderm may be explained by the fact that the phellem tissue once formed soon becomes suberized and ceases to function as living tissue. Von Mohl (1847) demonstrated that dead plant tissue loses moisture more rapidly than living tissue. Accordingly, the moisture content declines rapidly after the end of May to the latter part of June. In this connection it is of interest to note the graphs, Figures 14 and 15, representing the nitrogen changes during this period. Figure 14 shows that during the time when the periderm tissue is being built up, April and May, the non-amino, or protein, content is relatively high, 71.4 to 73.34 per cent of the total nitrogen; and Figure 15 indicates that the amino acids decline rapidly during the same period, 0.296 to 0.168 per cent on a dry weight basis. Altho further experimentation is necessary to decide this point, it appears possible that with the maturity, specialization, and differentiation of the periderm tissue, the non-amino nitrogen decomposes into the decomposition amino form. The latter undergoes a rise from 26.66 to 45.40 per cent of total nitrogen, and 0.168 to 0.286 per cent on a dry weight basis. This is shown in Figures 14 and 15.

In general, the periderm attains the first summer moisture maximum at the end of May and a second high peak is noticed in the middle of September before the autumnal yellowing of leaves sets in. During the first part of the period of heaviest rainfall, there is a sharp decline in the moisture of the periderm tissue. The cortex-phloem is most subject to fluctuation within the summer maximum, the outer xylem is less variable, and the inner xylem-pith maintains a fairly constant maximum.

Transition Between Growing and Dormant Periods

The most striking phenomenon during the transition period, September and October, is the sudden temporary decline in percentage of moisture content in all the complex tissues after the middle of September. The falling off in moisture begins while the leaves are still green, after the middle of September. When the fall minimum is reached, about the middle of October, the leaves are still green. The leaf blades were practically brown, and the petioles were colored red with anthocyanin by October 23, when a new moisture maximum was reached by all the complex tissues. When the fall maximum has been reached, growth has practically ceased and storage has been completed. At this time the moisture content of the inner xylem-pith is slightly greater than that of the outer xylem. Craib (1918) made similar observations for *Acer pseudoplatanus* later in the season. No direct evidence is offered to explain the temporary decline in moisture content during this period. The change is undoubtedly bound up with the chemical and physical changes that take place with the seasonal transformations. The drop takes place in spite of sufficient rainfall, as indicated in Figure 5. Further experimentation is necessary to clear up this matter.

Dormant Season—October to April

Various workers have reported experiments that have a bearing on the variation in moisture content of the twigs of trees during the winter. Water loss through transpiration, absorption of moisture from the atmosphere, water conduction through the wood, loss of dry weight by respiration during the winter, and translocation of material would influence the relative proportion of moisture in the various complex tissues as expressed in per cent dry weight.

As early as 1875, Wiesner and Pacher proved that 1-5 year horse-chestnut twigs transpired an appreciable amount of moisture in winter at a temperature of 13.17 degrees C., and a slight amount also at —30 degrees C. Table III is adapted from Wiesner and Pacher, showing the amount of water loss after 24-hour, weekly, and monthly periods at a temperature of 13.5 to 17.5 degrees C. The figures show conclusively that leaf traces favor transpiration as compared with the neighboring periderm; and that one-year portions of twigs are protected against transpiration through the periderm to a greater extent than 2- and 3-year twigs.

TABLE III

LOSS OF WATER FROM HORSE-CHESTNUT TWIGS *(Aesculus hippocastanum)*, JANUARY, UNIVERSITY OF VIENNA

Expressed in per cent of the Original Weight of the Twig

(Adapted from Wiesner and Pacher, 1875)

	1-Year twigs		2-Year twigs		3-Year twigs		5-Year twigs
	No leaf traces	Leaf traces present	No leaf traces	Leaf traces present	No leaf traces	Leaf traces present	Leaf traces not distinguishable
After 24-hour periods	0.836	1.583	0.965	1,268	1.105	1.206	0.641
	.836	1.531	1.081	1.326	1.126	1.242	.641
	.836	1.688	1.390	1.563	1.294	1.228	.603
	.662	1.490	1.181	1.312	1.094	1.152	.549
	.767	1.320	1.043	1.238	1.043	1.052	.573
	.550	1.295	0.965	1.230	1.021	1.053	.505
	0.650	1.343	1.236	1.239	1.023	1.075	0.493
After one week	5.122	10.250	7.861	9.76	7.706	8.008	4.005
After 30 days	16.376	31.741	23.551	28.879	23.837	25.219	11.407

The work of R. Hartig (1883) showed that twigs of deciduous trees and coniferous evergreens lose perceptible quantities of water when exposed outdoors in April. He also observed that these twigs gained in moisture during rainy weather. These results were verified by Kny (1895), who found that defoliated twigs lost water by transpiration, but may also absorb water slowly from the atmosphere. Bailey (1896) reported that apple twigs lose appreciable amounts of moisture in winter in western New York. The work of Sandsten (1904), at Madison, Wisconsin, established the fact that the loss of moisture varied from about 2 per cent to nearly 15 per cent in the two observed winters when 8-year-old apple trees were cut off, exposed outdoors, and weighed at intervals during the winter, December to April.

The recent work of Hildreth (1926) at St. Paul, Minnesota, on winter dessication of severed terminal apple twigs, sealed with grafting wax on the cut surface and exposed during the winter and weighed outside at intervals, shows that the twigs of the two varieties used in the experiment lost weight during practically the entire period. The only break occurred after a rain in February when a sample which had lost more moisture by reason of longer exposure, gained weight. This gain in weight during rainy weather is in harmony with the results of R. Hartig (1883) and Kny (1895). Hildreth reports that the rate of loss was gradual during periods of low temperature, but increased as spring opened despite the fact that the moisture content of the shoots was being constantly diminished. Except for the rainy period in February, the evaporation curve of twigs agrees fairly closely with the temperature curve. "Wealthy" twigs outdoors lost 29.3 per cent of the original weight between January 1 and April 8, altho nearly two-thirds of this loss occurred during the last month.

Sachs (1860a) pointed out that the freezing of the soil retards moisture absorption by trees in winter. According to Müller-Thurgau (1886), the soil and the woody stem of the tree in winter are poor conducting channels and unable to make good the water lost by evaporation from ice crystals in the tissues. This apparently explained to him the fact that twigs of apple and other trees lost weight when exposed outdoors on two consecutive cold nights. That roots exert only a minor influence on the water content of leaves in winter, is indicated by the experiments of Ivanoff (1924), at Petrograd (Leningrad), with evergreen trees cut from the roots. According to this worker the relatively low temperature of the surface soil and the atmosphere tend to slow down the conduction of water in the wood of trees in winter. Conduction does not cease entirely, but is slowed down so greatly that the water supplied is not sufficient to cover the loss by transpiration. This condition leads to a marked decrease in moisture content of the tree.

Kosaroff (1901), at Sofia, reported experiments that pointed to the fact that leafless twigs of trees both absorbed and transpired considerable quantities of water during winter at temperatures down to 0 degrees C. Therefore there must be movement of water in the twig. This conclusion seems in harmony with the work of Hildreth (1926) with apple twigs. "McIntosh" twigs severed from the tree, sealed on the cut surface, and exposed outdoors from December 17 to March 3, showed a moisture content of 34.5 per cent; the shoots left on the tree contained 45.5 per cent moisture on the same date. Hildreth concludes that trees in winter may be able to make up in part the moisture loss occurring from evaporation. He explains, however, that the temperature of the air and possibly of trunk and branches was frequently above freezing during the period.

Another factor influencing the relative proportion of moisture in the twigs of trees as expressed in per cent dry weight is the loss of combustible material in respiration. A decrease of dry weight without a proportionate decrease in moisture apparently indicates an increase in moisture content. That terminal apple twigs lose a significant amount of their dry weight by respiration during the winter is shown by the work of Beaumont and Willaman (1924), at St. Paul, Minnesota. These workers measured the amount of CO_2 given off by terminal apple twigs on the tree in February and March. De Long (1927), working in the same locality with excised apple twigs, reports similar results. The table below shows the amount of CO_2 given off on the basis of 24-hour periods, per 100 grams of material:

Temperature degrees C.	CO_2 given off mg.
−6	12
+6	48

Still another factor that may have an appreciable effect upon the relative proportion of moisture in the twigs of trees as expressed on a dry weight basis should be mentioned. There is the possibility of a change in dry weight taking place as a result of the translocation of material to or from a region during the winter season. There is, however, apparently no information available on the subject of the transport of material in dormant twigs during the winter.

The work of the authorities quoted shows that at least five factors may be operative during the winter season that might influence a change in the moisture content of woody twigs as expressed on a dry weight basis: (1) loss of water by transpiration, (2) a tendency to make good this loss in part by conduction of moisture through the wood from the root, (3) a tendency to absorb moisture from the atmosphere, especially in rainy weather, (4) diminution of total dry weight by respiration, and (5) increase or decrease in dry weight due to translocation of material during the winter. The moisture relations of the complex tissues of the apple twig during the winter must be interpreted in the light of these dynamic changes.

During the dormant season, end of October to April, there is a gradual to rapid decline in moisture in the various tissues, depending upon the nature of the complex tissue, and later a rise in two of the complex tissues.

In taking up the consideration of complex tissues from the outside to the center of the twig, we notice that in the periderm there is a sharp falling off in moisture content throughout the whole dormant period. The rate of loss is slowed down somewhat after the latter part of December. This continued moisture loss is probably due to the fact that the phellem is gradually dying or is dead tissue during this period. There is a rapid rise in March and April with the renewed activity of the phellogen.

After active growth ceases in the fall, the cortex-phloem is on the decline during the winter. This may have a possible bearing upon the moisture relations of this complex tissue. The cortex-phloem shows first a marked decrease (40.15 per cent on dry weight basis) in moisture content to the end of January and then an equally rapid increase in moisture content through February and March.

When the woody tissues are considered, a fairly gradual decline in moisture content of the outer xylem is noticed until March. The inner xylem-pith shows a fairly important loss of moisture until the latter part of December and then a fairly important gain until the end of February. During the whole period the cortex-phloem has a higher and the periderm a lower moisture content than the xylem tissues. The fall in moisture content from October to December or January may be due to water loss by transpiration, as explained by Ivanoff (1924). With the lowering of the temperature to the minimum in January, water conduction is slowed down so greatly that the moisture supplied is not sufficient to cover the loss by transpiration, leading to a marked decrease in moisture content in the complex tissues. Altho the dry weight is cut down by respiration during the same period, the experiments of Beaumont and Willaman (1924) and De Long (1927) show that the amount of CO_2 respired decreases markedly with the lowering of the temperature. The net result is therefore a decrease in moisture on a dry weight basis in spite of an actual decrease in dry weight. The increase in moisture in the cortex-phloem through February is probably due to increased water conduction with the gradual increase in temperature. Water absorption from the atmosphere may also influence the moisture content of the twig, as emphasized by R. Hartig (1883) and Kny (1895), but it is impossible to estimate the relative importance of this factor without further experimentation. The relatively greater losses or gains in moisture by the periderm and cortex-phloem may be due to their greater exposure to external conditions, or to the nature of the tissues, as has been suggested.

These individualities of the separate complex tissues, however, naturally disappear when the moisture is expressed as per cent of dry weight of the entire twig. On this basis the results agree in general with those of Hildreth (1925) with terminal apple twigs of "Oldenburg," the winter-hardy parent of "University." Hildreth made his observations in the same locality in 1923-24. There is a very gradual decline of moisture until the end of January, and then a very gradual increase to the end of February. Between the end of October and the end of January there is a maximum fall of a little over 10 per cent on a dry weight basis. This harmonizes with the results of Sandsten (1904). From the end of January to the end of February there is a rise of a little less than 2 per cent. From the end of December to the end of February the moisture is, therefore, practically constant when expressed on a dry weight basis.

It was emphasized earlier in this paper that the variation in the relative proportions of the tissues made it impossible to obtain a true conception of the moisture relations by analyzing the entire twig. There is considerable variation in the relative proportions of the complex tissues, as shown in Figure 4. On the basis of the entire twig, the picture presented follows that of the outer xylem fairly closely. The rapid fall and rise of moisture in the cortex-phloem during the winter and the important continual decline of moisture in the periderm, are entirely masked.

Transition Between Dormant and Growing Periods

During the transition between the dormant and the growing periods, in March and April, before active growth begins, there is a general tendency for the cortex-phloem and xylem tissues to gain moisture after the latter part of March and early April. The periderm shows a continuous gain from the beginning to the end of the period.

The marked rise in moisture content begins in early April before there is much rainfall, for only 0.39 inch of precipitation is recorded between April 4, the date of minimum moisture content for the cortex-phloem and xylem tissues, and April 18, when the marked rise in moisture is already fairly under way, as shown in Table II and Figure 5. At this time the reserve of moisture in the soil is probably sufficiently abundant to supply all the needs of the tree. The temporary decline at the end of March is, therefore, apparently not bound up with the absolute amount of rainfall, but is dependent on the chemical and physical transformations in the twig.

REGIONAL AND SEASONAL DISTRIBUTION OF CARBOHYDRATES

Microchemical determinations of the various carbohydrate fractions of the tissues of woody plants have been made quite extensively in the past. Macrochemical analyses of the chemical constituents of the complex tissues of such plants are, however, apparently rare and fragmentary. Niklewski (1906), at Leipzig, analyzed the cortex-phloem and wood of various woody plants for ether extract and sugars in an attempt to determine the rôle of fat in the transformations taking place during the winter period. Proebsting (1925) analyzed the cortex-phloem and xylem tissues of apple twigs for certain carbohydrate fractions and nitrogen from April to September, in making a study of the relation of stored food to cambial activity.

This section is devoted to a consideration of the evidence showing variation in the reserve carbohydrate constituents in the four complex tissues of the 2-3 year portions of the apple twig—periderm, cortex-phloem, outer xylem, and inner xylem-pith. For comparative purposes these data have also been calculated on the basis of the entire twig.

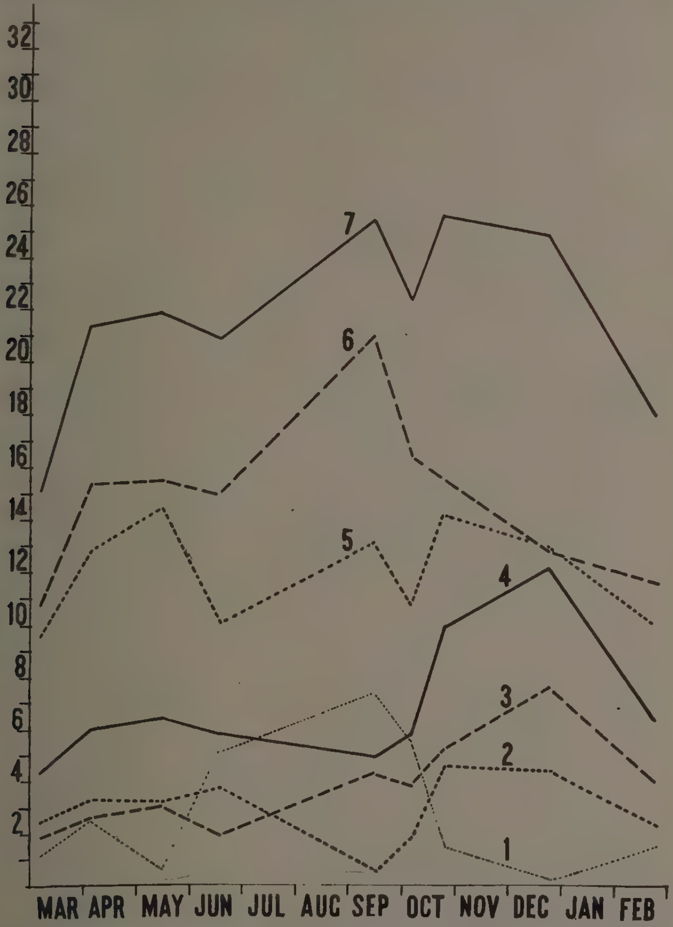

Fig. 6. Seasonal distribution of carbohydrates in periderm; acid-hydrolyzable hexosans (1); non-reducing sugars (2); reducing sugars (3); total sugars (4); pentosans (5); acid-hydrolyzable alcohol-insoluble carbohydrates (6); and total carbohydrates, except cellulose (7). Expressed in per cent dry weight.

The results of the macrochemical analyses—total carbohydrates, acid-hydrolyzable hexosans, reducing sugars, non-reducing sugars, and total sugars—are given in Tables IV, V, VI, VII, and VIII on a dry weight basis. In Table IX the total sugars, acid-hydrolyzable hexosans, and pentosans are expressed in per cent total carbohydrates except cellulose. The data are shown graphically in Figures 6 to 13.

TABLE IV

REGIONAL AND SEASONAL DISTRIBUTION OF SUGARS IN 2-3 YEAR PORTIONS OF APPLE TWIGS, MARCH 7, 1925, TO FEBRUARY 26, 1926

Expressed in per Cent Dry Weight

Date	Periderm	Cortex-phloem	Outer xylem	Inner xylem-pith	Whole twig
		Total Sugars			
March 7	4.39	9.82	3.33	3.23	4.50
April 4	6.00	5.51	1.20	1.37	2.45
May 16	6.39	4.12	0.89	1.06	2.02
June 20	5.93	5.61	0.81	0.83	1.97
September 17	4.90	5.46	0.57	0.71	1.67
October 10	5.87	7.42	0.91	0.96	2.51
October 23	9.83	12.07	1.74	2.27	3.89
December 23	12.04	13.17	5.86	8.11	8.31
February 26	6.37	8.87	4.29	6.16	6.49
		Reducing Sugars			
March 7	1.94	6.32	1.12	1.62	2.23
April 4	2.62	2.86	0.71	0.62	1.24
May 16	3.14	2.49	0.50	0.77	1.18
June 20	2.08	3.82	0.40	0.70	1.15
September 17	4.24	4.02	0.34	0.44	1.19
October 10	3.92	4.80	0.46	0.62	1.58
October 23	5.18	8.01	0.70	0.81	2.09
December 23	7.60	8.93	2.49	3.68	4.35
February 26	3.99	5.54	1.80	2.78	3.24
		Non-Reducing Sugars			
March 7	2.45	3.50	2.21	1.61	2.27
April 4	3.38	2.65	0.49	0.75	1.21
May 16	3.25	1.63	0.39	0.29	0.84
June 20	3.85	1.79	0.21	0.13	0.82
September 17	0.66	1.44	0.23	0.27	0.48
October 10	1.95	2.62	0.45	0.34	0.93
October 23	4.65	4.06	1.04	1.46	1.80
December 23	4.44	4.24	3.37	4.43	3.96
February 26	2.38	3.33	2.49	3.71	3.25

TABLE V

REGIONAL AND SEASONAL DISTRIBUTION OF ACID-HYDROLYZABLE HEXOSANS IN 2-3 YEAR PORTIONS OF APPLE TWIGS, MARCH 7, 1925, TO FEBRUARY 26, 1927

Expressed in per Cent Dry Weight

Date	Periderm	Cortex-phloem	Outer xylem	Inner xylem-pith	Whole twig
March 7	1.19	3.22	7.27	9.00	6.60
April 4	2.59	4.74	7.08	10.29	7.22
May 16	1.04	2.71	0.99	6.76	2.94
June 20	4.98	4.46	5.69	8.29	6.26
September 17	7.36	6.18	4.84	5.23	5.31
October 10	5.61	7.08	5.77	3.95	5.36
October 23	1.49	1.30	7.01	7.77	6.14
December 23	0.24	0.69	3.13	3.16	2.53
February 26	1.53	2.36	4.52	5.06	4.54

TABLE VI

REGIONAL AND SEASONAL DISTRIBUTION OF PENTOSANS IN 2-3 YEAR PORTIONS OF APPLE TWIGS, MARCH 7, 1925, TO FEBRUARY 26, 1926

Expressed in per Cent Dry Weight

Date	Periderm	Cortex-phloem	Outer xylem	Inner xylem-pith	Whole twig
March 7	9.53	13.66	20.49	16.81	17.29
April 4	12.84	11.04	22.07	20.70	18.82
May 16	14.49	14.74	23.56	21.17	20.40
June 20	10.02	14.02	22.02	22.52	19.94
September 17	13.14	14.02	22.91	22.93	20.91
October 10	10.74	12.17	22.35	23.25	19.87
October 23	14.19	16.53	21.30	20.80	20.11
December 23	12.47	15.82	22.10	21.84	20.30
February 26	9.99	15.12	19.84	21.78	20.90

TABLE VII

REGIONAL AND SEASONAL DISTRIBUTION OF ACID-HYDROLYZABLE ALCOHOL-INSOLUBLE CARBOHYDRATES (ACID-HYDROLYZABLE POLYSACCHARIDES) IN 2-3 YEAR PORTIONS OF APPLE TWIGS, MARCH 7, 1925, TO FEBRUARY 26, 1926

Expressed in per Cent Dry Weight

Date	Periderm	Cortex-phloem	Outer xylem	Inner xylem-pith	Whole twig
March 7	10.72	16.88	27.76	25.81	23.89
April 4	15.41	15.78	29.15	30.99	26.04
May 16	15.53	17.45	24.55	27.93	23.34
June 20	15.00	18.48	27.71	30.81	26.20
September 17	20.50	20.20	27.75	28.16	26.22
October 10	16.35	19.25	28.12	27.20	25.23
October 23	15.68	17.83	28.31	28.57	26.25
December 23	12.71	16.51	25.23	25.00	22.83
February 26	11.52	17.48	24.36	26.84	22.87

TABLE VIII

REGIONAL AND SEASONAL DISTRIBUTION OF ACID-HYDROLYZABLE ALCOHOL-INSOLUBLE CARBOHYDRATES PLUS TOTAL ALCOHOL-SOLUBLE CARBOHYDRATES IN 2-3 YEAR PORTIONS OF APPLE TWIGS, MARCH 7, 1925, TO FEBRUARY 26, 1926

Expressed in per Cent Dry Weight

Date	Periderm	Cortex-phloem	Outer xylem	Inner xylem-pith	Whole twig
March 7	15.11	26.70	31.09	29.04	28.39
April 4	21.41	21.29	30.35	32.36	28.49
May 16	21.92	21.57	25.44	28.99	25.36
June 20	20.93	24.09	28.50	31.64	28.17
September 17	25.40	25.66	28.32	28.87	27.89
October 10	22.22	26.67	29.03	28.16	27.74
October 23	25.51	29.90	30.05	30.84	31.14
December 23	24.75	29.68	31.09	33.11	31.14
February 26	17.89	26.35	28.65	33.09	29.36

TABLE IX

Regional and Seasonal Distribution of Total Sugars, Pentosans, and Acid-Hydrolyzable Hexosans, in 2-3 Year Portions of Apple Twigs, March 7, 1925, to February 26, 1926

Expressed in per Cent of Total Reserve Carbohydrates

Date	Periderm	Cortex-phloem	Outer xylem	Inner xylem-pith	Whole twig
		Total Sugars			
March 7	29.05	36.77	10.71	11.12	15.85
April 4	28.02	25.88	3.95	4.23	8.59
May 16	29.15	19.10	3.49	3.65	7.96
June 20	28.33	23.28	2.84	2.62	6.99
September 17	19.29	21.27	2.01	2.45	5.98
October 10	26.41	27.82	3.13	3.40	9.04
October 23	38.53	40.37	5.79	7.36	12.49
December 23	48.64	44.37	18.84	26.06	26.68
February 26	35.60	33.66	14.97	18.61	22.10
		Pentosans			
March 7	63.08	51.16	65.90	57.88	60.83
April 4	59.97	51.85	72.71	63.96	66.05
May 16	66.10	68.33	92.61	73.02	80.44
June 20	47.87	58.19	77.26	71.17	70.78
September 17	51.73	54.63	80.89	79.42	74.97
October 10	48.33	45.63	76.98	82.56	71.62
October 23	55.62	55.28	70.88	67.44	64.57
December 23	50.38	53.30	71.08	70.08	65.18
February 26	55.84	57.38	69.24	65.82	71.18
		Acid-Hydrolyzable Hexosans			
March 7	7.87	12.05	23.38	30.99	23.24
April 4	12.09	22.26	23.32	31.79	25.34
May 16	4.74	12.56	3.89	23.31	11.59
June 20	23.79	18.51	19.96	26.20	22.22
September 17	28.97	24.08	17.09	18.11	19.03
October 10	25.24	26.54	19.87	14.02	19.32
October 23	5.84	4.34	23.32	25.19	19.71
December 23	0.96	2.32	10.06	10.15	8.15
February 26	8.55	8.95	15.77	15.29	15.46

Total Carbohydrates

The total amount of reserve carbohydrates in 2-3 year portions of apple twigs is quite large, as shown in Table VIII and Figures 6 to 10 inclusive. The magnitude of this reserve material is apparently directly proportional to the nearness to the center of the twig. The highest per cent, from 28.16 to 33.11 on a dry weight basis, is found in the inner xylem-pith. The percent in the outer xylem, from 25.44 to 31.09, is only slightly lower than that of the tissue which it surrounds; the per cent in the cortex-phloem, from 21.29 to 29.90, is lower than that of the outer xylem, and the corresponding value for the periderm is below that of the cortex-phloem.

On the basis of the entire twig, the tendency of the outer xylem is reflected except from September to December, when the high carbohydrate content of the cortex-phloem makes possible a maximum in October for the twig as a whole. This is shown in Table VIII and Figure 10.

At the end of the dormant season there is a marked decline in the total reserve carbohydrates in most of the complex tissues of 2-3 year portions of apple twigs. In the cortex-phloem there is a rapid decline after the latter part of December, in the outer xylem the decline is steady but less marked, and in the inner xylem-pith there is a rise during March that is probably due to translocation of reserve carbohydrates from other parts of the tree and a lesser or later utilization of stored materials. The minimum in reserve carbohydrates is

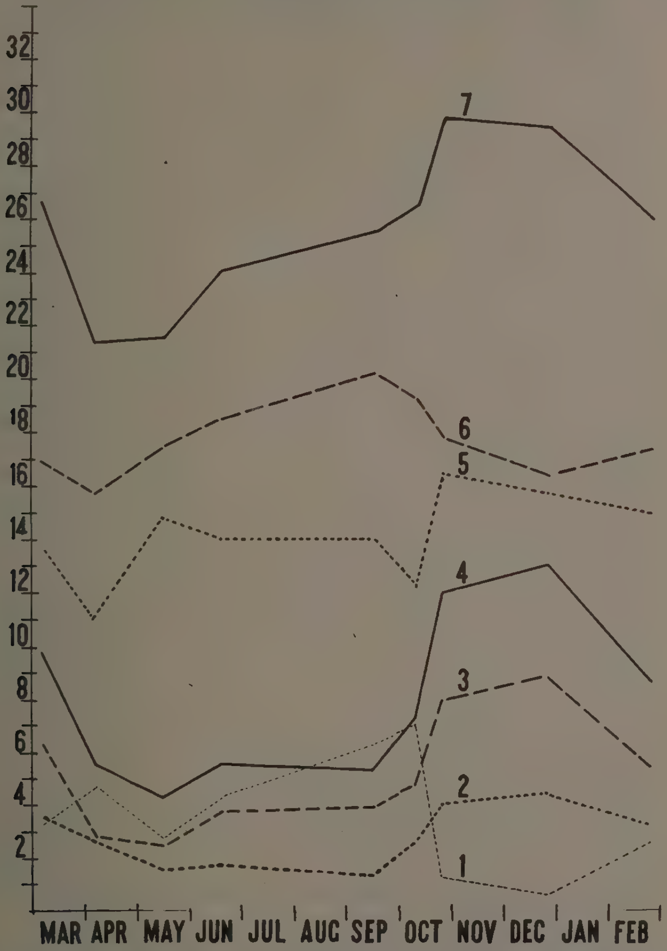

Fig. 7. Seasonal distribution of carbohydrates in cortex-phloem; acid-hydrolyzable hexosans (1); non-reducing sugars (2); reducing sugars (3); total sugars (4); pentosans (5); acid-hydrolyzable alcohol-insoluble carbohydrates (6); and total carbohydrates, except cellulose (7). Expressed in per cent dry weight.

reached during April and May for the cortex-phloem and about the middle of May for the outer xylem and inner xylem-pith.

The periderm shows a difference in trend of reserve carbohydrates at the end of the dormant season and at the time of the initiation of growth in spring. There is a rise until the middle of May with a slight decline in June. This is probably due to the nature of the periderm tissue, as explained in the section devoted to moisture distribution.

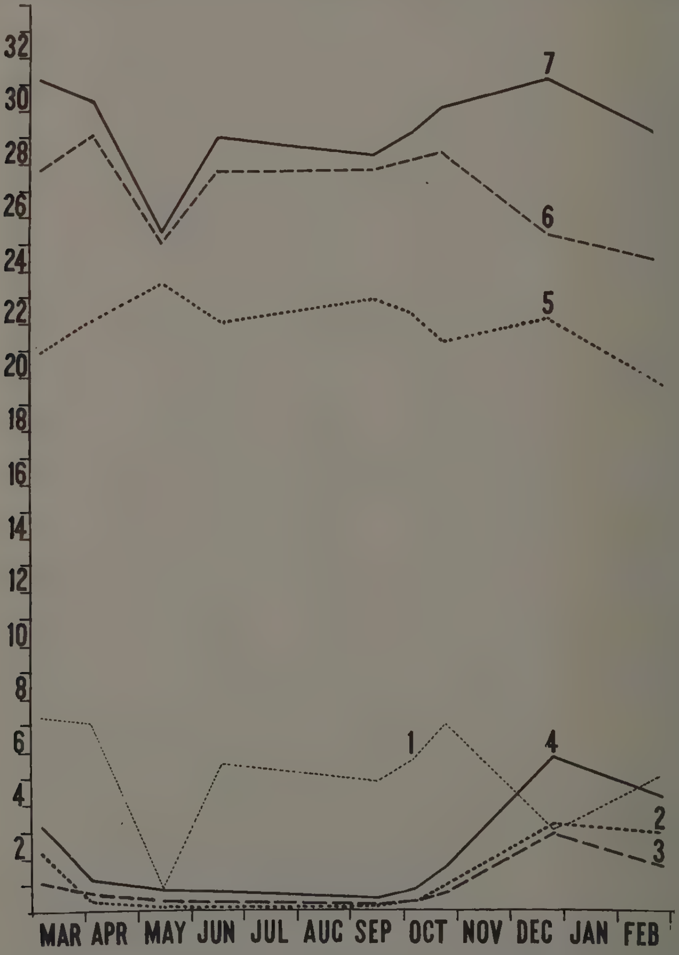

Fig. 8. Seasonal distribution of carbohydrates in outer xylem; acid-hydrolyzable hexosans (1); non-reducing sugars (2); reducing sugars (3); total sugars (4) pentosans (5); acid-hydrolyzable alcohol-insoluble carbohydrates (6); and total carbohydrates, except cellulose (7). Expressed in per cent dry weight.

The marked decline in stored or reserve carbohydrates in all the complex tissues except the periderm, at the time growth is initiated, is undoubtedly due to the utilization of the reserves in growth extension. This statement is in harmony with the work of Puriewitsch (1898), who maintains that organic materials move from the storage tissues to other regions when the transported materials are utilized in the tissues receiving them. Translocation of stored organic materials from a region also takes place when like organic substances move through the region to more distant consuming tissues.

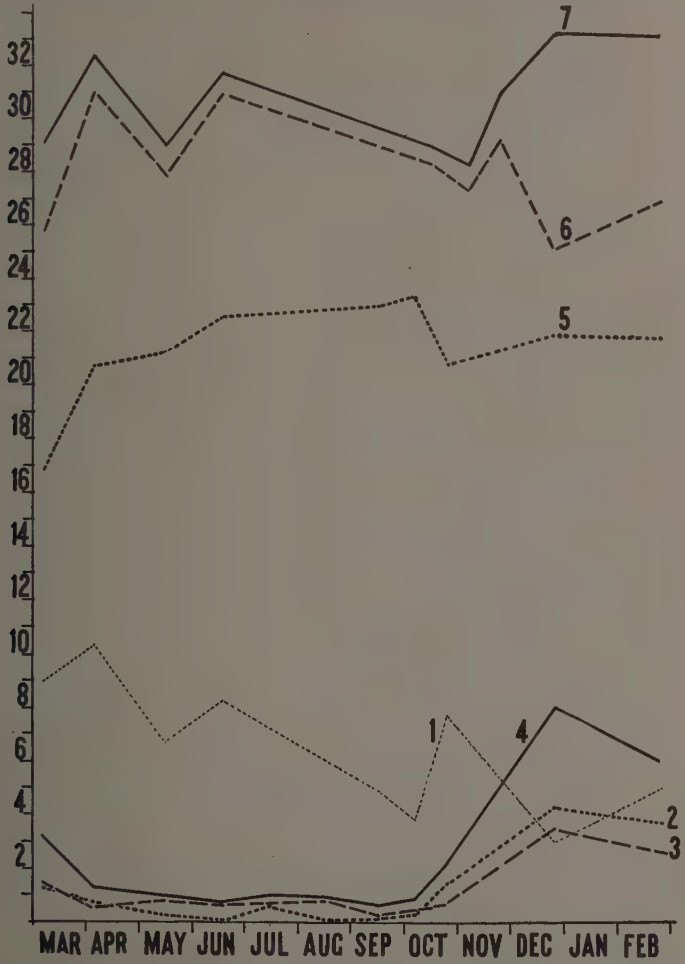

Fig. 9. Seasonal distribution of carbohydrates in inner xylem-pith; acid-hydrolyzable hexosans (1): non-reducing sugars (2); reducing sugars (3); total sugars (4); pentosans (5); acid-hydrolyzable alcohol-insoluble carbohydrates (6); and total carbohydrates, except cellulose (7). Expressed in per cent dry weight.

The following phenological data are of interest in this connection:

Date	Development of "University" Apple Trees, Spring 1925
March 23	Trees dormant
April 4	Fruit buds beginning to swell
April 18	Fruit buds partially expanded
May 2	Fruit buds fully expanded; flower petals pink, and leaves ¾ inch wide
May 16	Trees in full bloom; new terminal branches 3 inches long.

Reference to Table VIII and Figures 6, 7, 8. and 9 reveals the fact that as the development of new shoots progresses the total reserve carbohydrates in the complex tissues decrease toward a minimum except in the periderm, which seems to draw on the carbohydrate supply at this time. When the fruit buds are beginning to swell, in early April, the reserve carbohydrates in the cortex-phloem have fallen to the minimum, as shown in Figure 7. When the trees are in full bloom and the new terminal shoots are 3 inches long, the reserve carbohydrates in the xylem tissues have declined to a minimum by the middle of May, as indicated in Figures 8 and 9.

The marked increase in total reserve carbohydrates in all the complex tissues except the periderm, after the middle of May, is ascribable to the net gain from the photosynthetic process in the leaves. Surplus carbohydrates are transported to the stem and accumulate as reserves.

In the periderm there is a rapid building up of reserve carbohydrates after the latter part of June. In the cortex-phloem the rise of carbohydrates is consistent during the entire growing season; in the outer xylem there is a very slight decline to September after a maximum is reached in June. The inner xylem-pith follows the trend of the outer xylem, but the decline from June to September is more marked.

The transition between the growing season and the dormant period, September to October, is characterized by carbohydrate accumulation in the various complex tissues. From the standpoint of total carbohydrates, Combes and Kohler (1922) have shown that from 1/5 to 1/4 of the soluble carbohydrates in the leaves is transported to the living parts to build up a reserve. The translocation of this material is reflected in a very marked increase in the cortex-phloem and the inner xylem-pith, a rise of 4.24 per cent from September 17 to October 23 in the cortex-phloem, and of 4.95 per cent from October 10 to September 23, in the inner xylem-pith. In the cortex-phloem the maximum is reached in the latter part of October, but in the xylem tissues the maximum is not reached until December. Apparently considerable time elapses after the leaves have fallen before translocation to the various storage tissues is completed.

After the maximum is reached, in October or December, there is a decline in carbohydrates, the rate varying with the particular complex tissue.

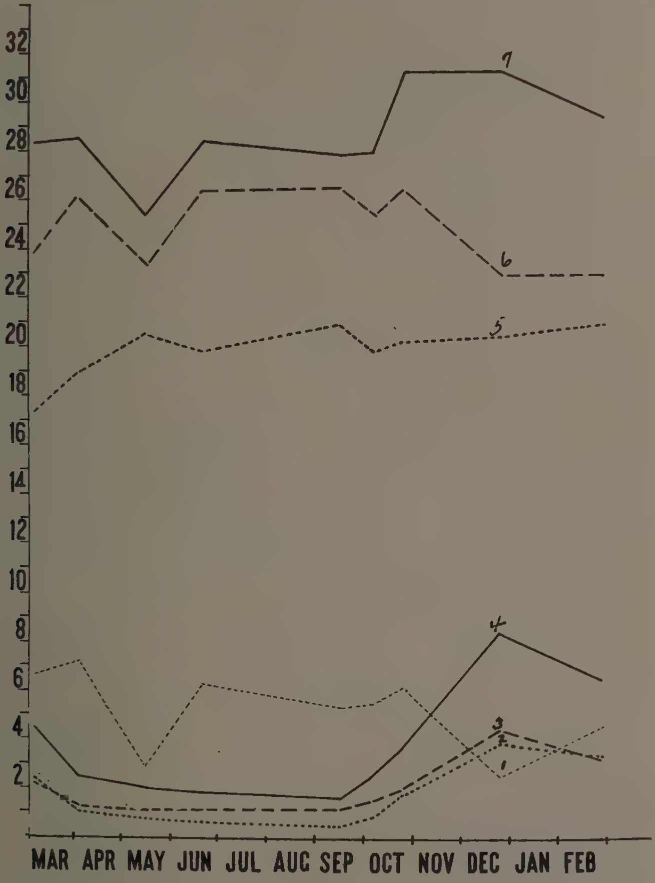

Fig. 10. Seasonal distribution of carbohydrates in the entire 2-3 year portion of the twig; acid-hydrolyzable hexosans (1); non-reducing sugars (2); reducing sugars (3); total sugars (4); pentosans (5); acid-hydrolyzable alcohol-insoluble carbohydrates (6); and total carbohydrates, except cellulose (7). Expressed in per cent dry weight.

In the periderm there is first a gradual decline during November and December, but from January on there is a rapid decline to a minimum in March. In the cortex-phloem the decline is very gradual between October and January, but the rate increases from this time until the minimum is reached, in May. In the outer xylem there is a marked decline from the December maximum to the May minimum.

In the inner xylem-pith there is first a very gradual decline from the December maximum to the end of February, and then a rise to a new maximum in March-April preceding the period of rapid growth extension, during which the minimum is reached in May.

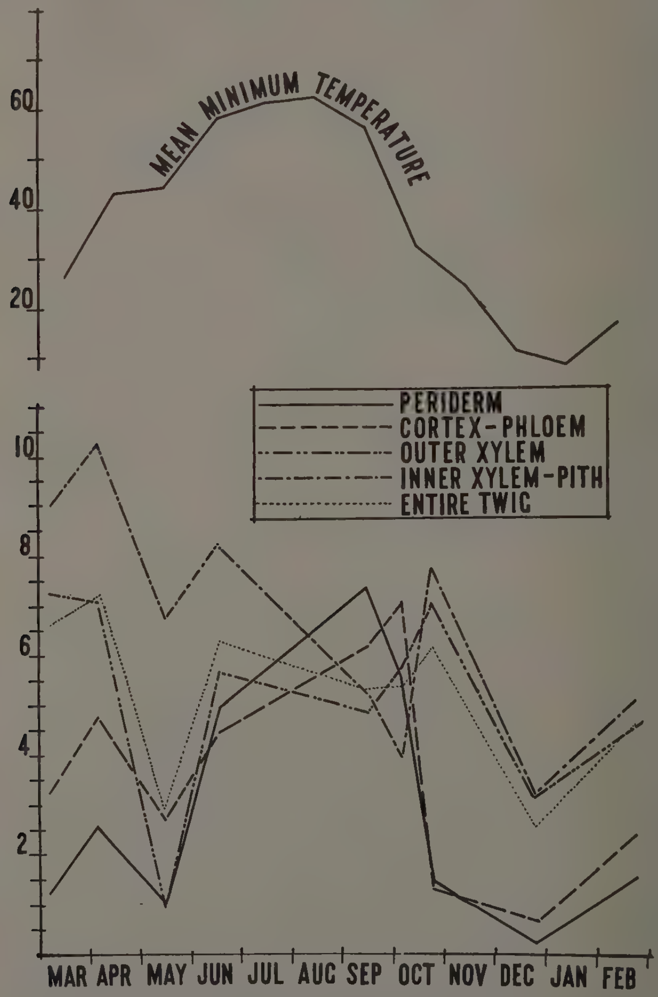

Fig. 11. Lower, seasonal distribution of acid-hydrolyzable hexosans in periderm, cortex-phloem, outer xylem, and inner xylem-pith. Expressed in per cent dry weight.
Upper, mean monthly minimum temperature, expressed in degrees Fahrenheit.

The decline in carbohydrates during the winter is apparently due largely to loss by respiration, as shown by the work of Beaumont and Willaman (1924) and De Long (1927). As the temperature begins to rise in February and March from the low level of December and

January, part of the rapid decline is probably due to loss through translocation of materials to the growing points.

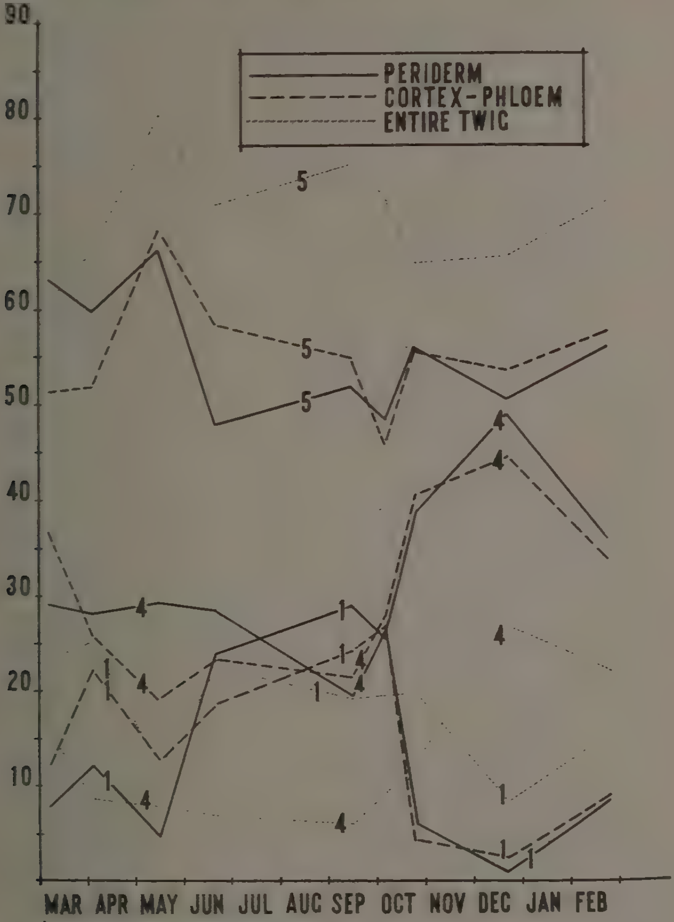

Fig. 12. Seasonal distribution of acid-hydrolyzable hexosans (1); total sugars (4); and pentosans (5), in periderm, cortex-phloem, and entire twig. Expressed in per cent of total carbohydrates.

Pentosans

A large proportion of the reserve carbohydrates of the complex tissues of 2-3 year portions of apple twigs consists of pentosans, as shown in Table IX and Figures 6 to 10, inclusive. The pentosan content of the xylem tissues, always over 55 per cent, is greater than that of the periderm and cortex-phloem, always over 45 per cent of the total reserve carbohydrates.

On the basis of total dry weight, there appear to be marked fluctuations in the pentosan content of the complex tissues of 2-3 year portions of apple twigs. At certain times of the year these fluctuations are, however, apparent rather than real. The rise in pentosans from April to May in all the tissues represents a relative diminution in the hexosans, as shown in Table IX and Figures 12 and 13, where the pentosans are expressed in per cent of total reserve carbohydrates.

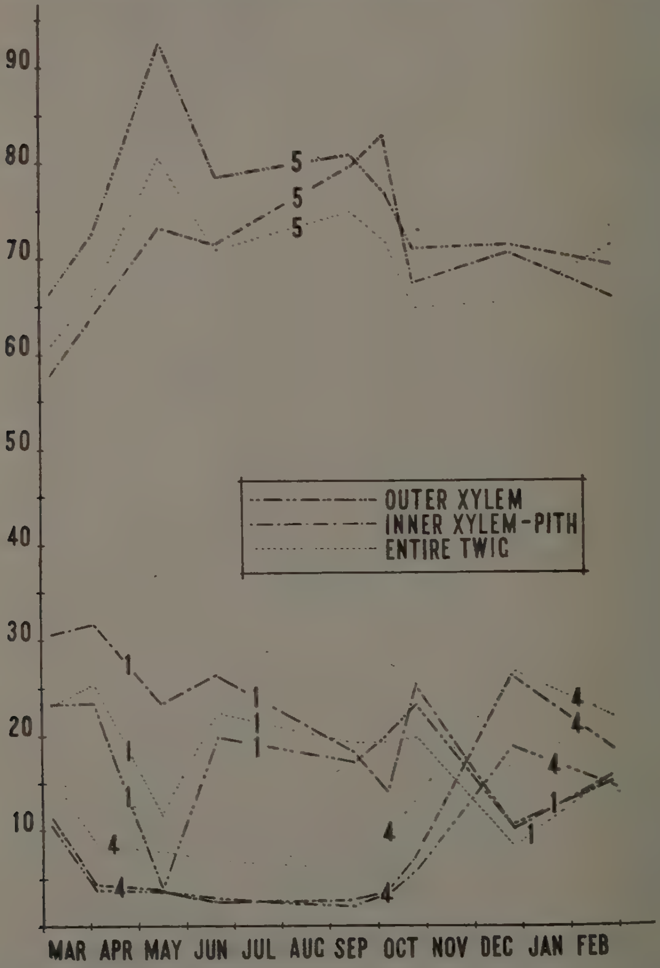

Fig. 13. Seasonal distribution of acid-hydrolyzable hexosans (1); total sugars (4); and pentosans (5), in outer xylem, inner xylem-pith, and entire twig. Expressed in per cent of total carbohydrates.

On the basis of total reserve carbohydrates, the relative proportion of pentosans in periderm and cortex-phloem remains fairly constant after the apparent spring rise in April-May as shown in Figure 12, except for the decline in September-October. In the xylem tissues the decline in pentosan content on the basis of total reserve carbohydrates does not take place until October. Between October and March this lower level is maintained.

The pentosan content is probably fairly constant. The apparent decline of pentosans in the woody tissues from October to March is due to the relatively great increase in total sugars preceding leaf-fall.

Acid-Hydrolyzable Hexosans and Sugars

The acid-hydrolyzable hexosans and sugars presumably play an important rôle in the economy of the apple tree. These are apparently the most labile types of reserve carbohydrates in the plant cell, and are probably in equilibrium with other forms of carbohydrates, especially sugars, changing from one to the other in response to such varying external and internal environmental conditions as changing concentrations of sugar solution, varying temperatures, presence of enzymes.

Sugars: Growing Period, April to September

During the growing season the sugar content is extremely small in the xylem tissues, always below 2 per cent between April 4 and October 10, but the amount of sugars is relatively much more abundant in the periderm and cortex-phloem, ranging from 4.90 to 6.00 and 4.12 to 7.42 per cent on a dry weight basis, during the same period, as shown in Table IV and Figures 6, 7, 8, and 9. On the basis of per cent total carbohydrates, the same relationship exists. There is a slight drop in the sugar content of the periderm from May to September. In the cortex-phloem, after the spring drop in April and May there is a rise to a new level in June. This level remains almost constant until September, when a rise to a new higher level begins.

The sugar content of the xylem tissues is relatively constant during the entire growing season, usually below 1 per cent until September, when a marked increase sets in.

In the periderm the reducing sugars are greater in amount than the non-reducing sugars after the middle of July; and in the cortex-phloem, outer xylem, and inner xylem-pith the non-reducing sugars are consistently lower than the reducing sugars during the growing period, as shown in Table IV and Figures 6, 7, 8, and 9.

Acid-Hydrolyzable Hexosans: Growing Period, April to September

In March-April, just before active growth begins, an acid-hydrolyzable hexosan maximum is attained, but with the beginning of active growth a marked decline begins, owing to the utilization of the hydrolyzed hexosans in growth extension. When the minimum hexosan content was reached, in the middle of May, the trees were in full bloom, and the new shoots 3 inches long. From this time forward the photosynthetic function of the leaves of the new shoots apparently not only produces sufficient carbohydrates for further growth extension but also furnishes a net gain to be stored in the form of hexosans, which rise markedly in all the tissues, as shown in Figures 6, 7, 8, 9, and 11. That this represents a relative gain as compared with other reserve carbohydrate fractions is shown in Figures 12 and 13, where hexosans are expressed in per cent total carbohydrates.

After the middle of June there is a steady increase in hexosans to a fall maximum in periderm and cortex-phloem in September-October. There is, however, a falling off of hexosan content in the woody tissues during the same period. That this is an actual falling off in relation to the other reserve carbohydrates is shown in Figure 13. The decline is relatively greater in the inner xylem-pith.

Acid-Hydrolyzable Hexosan-Sugar Transformation: Dormant Period, September to March

The marked rise in total carbohydrates as a result of translocation from the leaves, as shown by Combes and Kohler (1922), is due in large measure to the relatively important increase in sugars, which reach a new maximum in December in all the complex tissues. During the same period there is an equally marked decline in acid-hydrolyzable hexosans, which reach a minimum in December for all the tissues. This shows that the rise of sugar is due to two causes: (1) the translocation of carbohydrates from the leaves and (2) the transformation of acid-hydrolyzable hexosans into sugar. Various workers have reported experiments that have a bearing on the cause and the extent of hexosan-sugar transformations.

Causal Mechanism

Einhoff (1805) demonstrated that in the potato tuber the sugar content increases with low temperature. Vogel (1820) reported experiments showing that after freezing and thawing starch paste loses its sticking quality and its fluidity. These properties are again taken on when the material is brought to the boiling point of water. He also showed that frozen starch paste loses considerable water by syneresis. These experiments were repeated by Sachs (1860b) in an attempt to come closer to an understanding of the effect of temperature upon organic substances in the cell.

Butkewitsch (1908) demonstrated a maltose-splitting enzyme in the cortex-phloem of *Sophora japonica, Rabinia pseudoacacia, Caragana arborescens,* and *Populus nigra.* He also prepared a similar enzyme from the wood of *Sophora japonica.* From this evidence Butkewitsch naturally concluded that the end product of starch splitting in trees is glucose.

Butkewitsch (1908) also showed that toluol and chloroform lower or inhibit the synthetic activity of the starch-building plastids. He found that lowering the temperature has a similar effect. He recognized the analogy between the processes, and ascribed the building up of sugar to the decrease in the ability of the plastids to form starch at lower temperatures.

Czapek (1901) proved that low temperature decreases the ability of the plastids to build starch. Higher sugar concentrations are required for the plastids to build starch at 0 degrees C. than at 16 to 18 degrees C. From this information the conclusion can be drawn that starch already stored may be reconverted into sugar as the result of an equilibrium reaction when the temperature is lowered.

Coville (1920) explained the starch-sugar transformation in plants on exposure to low temperature as an increased permeability of the starch grain to enzymes, thus allowing the hydrolytic catalyst to come in contact with the starch. He does not explain the regeneration of starch with the increase in temperature.

The effect of temperature on the acid-hydrolyzable hexosan content of the complex tissues of 2-3 year portions of apple twigs is shown in Table V and Figure 11. With the drop in mean minimum temperature, beginning in September, there is a profound change in the total amount of acid-hydrolyzable hexosans in all the complex tissues. The periderm and cortex-phloem show a rapid decline from October 10 to October 23, reaching a minimum in December. In the woody tissues there is a rise from October 10 to October 23. This is probably due to the fact that much carbohydrate material is being transported into the wood from the leaves, and the concentration of sugar may be high enough to cause a temporary deposition of starch. With the further lowering of the temperature this starch will be hydrolyzed to sugars because at lower temperatures higher concentrations of sugar are required for plastids to build starch, as demonstrated by Czapek (1901). Consequently, the starch minimum is reached in December-January with the mean minimum temperature at the lowest point. The increase in mean minimum temperature after the middle of January is accompanied by a corresponding rise in the acid-hydrolyzable hexosans, as shown in Figure 11.

Extent of Acid-Hydrolyzable Hexosan Disappearance

According to Theodor Hartig (1858), the building up of a starch reserve in the tree at the time of leaf-fall is to be considered as ended when the living cells of the wood and ray parenchyma of the cortex-phloem and pith are packed with starch grains. This starch maximum he considered as remaining unchanged until spring, followed at the beginning of summer by a starch minimum. This viewpoint was held by prominent plant physiologists, including Pfeffer, until the 80's of the last century, in spite of the evidence to the contrary which accumulated after the 60's.

Famintzin and Borodin (1867) found low starch content in twigs of birch during winter. Twigs that were brought into the room built up starch in the same manner as twigs outside in the spring. These workers noticed that the starch disappears as growth begins, and expressed the opinion that starch formation is not due to translocation but is the result of the transformation of substances already present in the cells. Famintzin and Borodin frankly admitted that their experiments gave them no information as to what these substances are.

Reichardt (1871) noticed the absence of starch in winter (February) in single twigs of *Salix fusca, Tilia europaea,* and *Betula alba,* but he believed that these were exceptional cases, for he was dominated by the then prevalent theory that the reserve starch undergoes no transformation during the winter. He was apparently unaware of the work of Famintzin and Borodin (1867).

Russow (1882) at Dorpat, observed that little or no starch could be found in the cortex-phloem of many native trees and shrubs during the winter months (December, January, February), but oil or fat in the parenchymatous elements, which were packed with starch at the beginning and end of the growing period. In contrast, the parenchymatous elements of the wood were found to be as rich in starch in winter as at the end of the growing period.

Barenetzky and Grebnitzky (1884) explained that in certain trees there is a strach minimum in the cortex-phloem and wood during the winter, with a starch maximum in the fall and spring. According to these authorities the starch changes to oil in winter, and soft-wooded trees *(Tilia)* are entirely starch-free in winter; but in hard-wooded trees the starch disappears entirely only in the cortex-phloem. There is an abundance in the wood but the amount is somewhat reduced.

The classical work of Müller-Thurgau on the starch-sugar transformation in the potato with the lowering of the temperature appeared in 1882. Müller-Thurgau (1885) extended the theory built upon his work with the potato to explain the initiation and breaking of the rest period in trees. He maintained that "when the sugar transformation from the leaves stops then the development of the buds slows down and when the last sugar is transformed into starch then growth will cease. The rest period has begun. When in time starch is again changed to sugar by the action of low temperature then growth can take place again. Rest period is due to the fact that little or no sugar is available to the buds."

Alfred Fischer (1888, 1891), building upon the results of his own experiments, and those of his predecessors quoted above, but apparently unaware of the work of Famintzin and Borodin (1867), reported an extensive survey of the starch-oil and starch-glucose transformations in deciduous dicotyledonous and coniferous trees. On the basis of the principal reserve storage material during the winter, Fischer grouped trees into two classes. One group included trees in which the reserve starch that had accumulated during the growing season is changed to oil and to a lesser extent into glucose in the xylem and cortex-phloem at the beginning of winter. This group he named oil-storing trees or "Fettbäume" *(Betula, Tilia, Pinus sylvestris,* etc.). Another group included trees in which the reserve starch in the cortex-phloem is changed to glucose and perhaps another unknown substance, but the starch in the xylem-pith remains practically unchanged from fall to winter with slight fluctuations. This group he called starch-storing trees, or "Stärkebäume" *(Quercus, Ulmus, Acer, Pyrus, Sorbus,* etc.) In the "Stärkebäume," according to Fischer, there is but a very slight falling off of starch in the xylem-pith as compared with the fall maximum, so small, in fact, that all the rays may be colored black-blue with iodine during the winter months, and the starch disappears completely only in the cortex-phloem. In the cortex-phloem, Fischer recognized two starch maxima, fall and spring, and two starch minima, winter and May. In the xylem-pith he recognized only one starch minimum—in May—and a starch maximum from fall through the winter.

Niklewski (1906), at Leipzig, confirmed by means of macrochemical analyses the observations of Russow (1882) and Alfred Fischer (1891) on the starch-oil transformation in the "Fettbäume" during the winter.

The results, obtained by macrochemical analyses of 2-3 year portions of apple twigs, indicated in Tables IV, V, and IX, and Figures 6, 7, 8, 9, 11, 12, and 13, show that under central Minnesota conditions the acid-hydrolyzable hexosan content not only of the periderm and cortex-phloem but also of the woody tissues, is reduced materially during the winter, and that there is a marked rise in sugar during the same period. The results obtained in the case of one representative of the group of "Stärkebäume" do not show a high glucose content of the wood during the spring and summer nor a glucose minimum in the wood in winter, as reported by Fischer (1891). The difference in the results may be explained by a consideration of the technic used by Alfred Fischer in determining the glucose in the vessels of the wood. Fischer used his samples in the fresh condition or kept them in the dry state and soaked them with water before using. Twigs were split and put into a concentrated solution of copper sulphate for about 5 minutes; they were then rinsed with water and put into a boiling solution of Rochelle salt and sodium hydroxide for 2-5 minutes. The glucose reaction took place only in the outer layer of the wood, which was removed and the process repeated. Such a method evidently does not reach the glucose in the living cells and leaves non-reducing substances entirely out of account.

By the application of this method, Fischer found glucose relatively abundant in the vessels, or tracheids, of various kinds of trees during spring and summer, but relatively little or no glucose during winter. From the end of May to the starch minimum in the middle of the following May, he found abundant starch grains in the living cells of the wood, and therefore concluded that the starch of the xylem-pith does not change to sugar during the winter. Table V, however, shows that the hexosan content of the outer xylem is reduced almost by half between June 20 and December 23, and in the inner xylem-pith the reduction equals more than 50 per cent. Between October 23 and December 23 the decrease is even more marked. Figures 8 and 9 show that the sugars are correspondingly increased during the same period. These graphs also show that the non-reducing sugars are in excess over the reducing sugars in the xylem tissues. The fact that about 50 per cent of the hexosans remain unchanged in the xylem-pith during winter would tend to mask the situation so that microchemical observations apparently indicate that no change in starch content had taken place. Similarly, the glucose content of the tracheal vessels is probably so low in winter that the impression would be given that xylem tissues are poor in glucose. Fischer took no account of non-reducing sugars, which are in excess of glucose in the wood during winter in the particular apple trees under central Minnesota conditions. This explains the conclusion he arrived at and that he made the basis of his classification. If the facts shown in one of the "Stärkebäume" are representative of the rest of the group, it appears that the nomenclature adopted by Fischer is no longer adequate for the group as a whole. Sugar storage during the winter months is apparently more characteristic than hexosan storage in the xylem-pith as well as in the cortex-phloem of the particular apple trees under central Minnesota conditions. Figures 8, 9, 12, and 13 show conclusively that hexosan storage plays a minor rôle during winter as compared with the relative amount of total sugars present, in *Pyrus malus*. The term "Zuckerbäume," sugar-storing trees, appears to be a more appropriate name for these trees.

The facts presented show that the periderm and cortex-phloem differ from the outer xylem and inner xylem-pith with regard to acid-hydrolyzable hexosan maxima and minima. Table V and Figure 11 indicate two hexosan maxima and two minima for the periderm and cortex-phloem and three hexosan maxima and three minima for the outer xylem and inner xylem-pith.

Periderm and Cortex-Phloem

Fall maximum, September to October
Winter minimum, December to January
Spring maximum, March to April
Spring minimum, May

Outer Xylem and Inner Xylem-Pith

Summer maximum, June
Fall minimum, September to October
Fall maximum, October to November
Winter minimum, December to January
Spring maximum, March to April
Spring minimum, May

On the basis of the whole twig, as shown in Figure 10, the tendency of the outer xylem is reflected in the acid-hydrolyzable hexosan content, but the sugar content is greater than that of the outer xylem, owing to the high sugar content of the cortex-phloem.

REGIONAL AND SEASONAL DISTRIBUTION OF NITROGEN

Macrochemical studies of the regional and seasonal distribution of nitrogen in woody plants are apparently fragmentary and rare. Proebsting (1925) analyzed total nitrogen in the cortex-phloem and xylem of apple twigs from April to September in connection with his work on the relation of stored food to cambial activity in the apple. The work reported in this section is concerned with the distribution of the total organic and amino nitrogen fractions in the four complex tissues—periderm, cortex-phloem, outer xylem, and inner xylem-pith—of the 2-3 year portions of apple twigs throughout the year. The data are recorded in Tables X, XI, XII, and XIII, and are shown graphically in Figures 14 and 15.

Total Organic Nitrogen

The most striking fact brought out in Table X and the lower graph of Figure 14 is the extremely small amount of organic nitrogen in 2-3 year portions of apple twigs.

Table X shows that the organic nitrogen content of the complex tissues rarely rises above one per cent of the dry weight in the periderm and cortex-phloem and remains below 0.5 per cent at all times in the outer xylem and inner xylem-pith.

The lower graph of Figure 14 shows plainly that the periderm, cortex-phloem, outer xylem, and inner xylem-pith follow the same trend in organic nitrogen content. There are, however, differences in amount. The organic nitrogen content of the periderm and cortex-

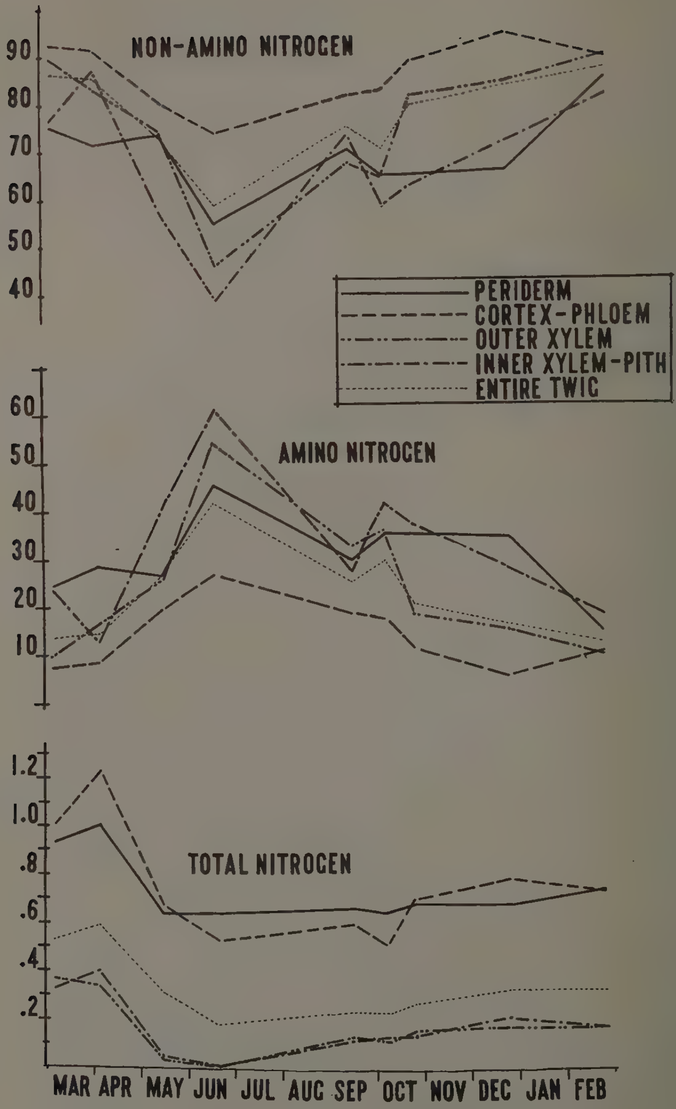

Fig. 14. Lower, seasonal distribution of total organic nitrogen in periderm, cortex-phloem, outer xylem, inner xylem-pith, and entire twig. Expressed in per cent dry weight. Upper, amino and non-amino nitrogen in the same complex tissues and the entire twig. Expressed in per cent of total organic nitrogen.

phloem is relatively much greater on a dry weight basis than that of the xylem tissues.

TABLE X

REGIONAL AND SEASONAL DISTRIBUTION OF TOTAL NITROGEN IN 2-3 YEAR PORTIONS OF APPLE TWIGS, MARCH 7, 1925, TO FEBRUARY 26, 1926

Expressed in per Cent Dry Weight

Date	Periderm	Cortex-phloem	Outer xylem	Inner xylem-pith	Entire twig
March 7	0.93	1.15	0.37	0.33	0.53
April 4	1.04	1.27	.35	.41	.59
May 16	0.63	0.67	.18	.20	.31
June 20	.63	.52	.07	.05	.17
September 17	.65	.59	.11	.13	.22
October 10	.63	.45	.13	.11	.22
October 23	.67	.69	.15	.17	.26
December 23	.67	.78	.20	.18	.32
February 26	0.74	0.73	0.18	0.18	0.32

The maximum in organic nitrogen reserves is reached in all the complex tissues during March-April. This maximum is no doubt partly due to the relative decrease in carbohydrates in the cortex-phloem. In the other tissues there is no decrease of carbohydrates but rather an increase in March-April.

The organic nitrogen reserves are at the highest just preceding the initiation of new growth. Rippel (1923) has reported experiments with *Sambucus nigra* showing that during the first spring growth translocation of nitrogen from the stem to the young shoots and leaves is very marked. A similar translocation from the apple twig would account for the rapid decline of organic nitrogen in spite of the fact that the total reserve of carbohydrates also shows a rapid decrease from April to May in some of the complex tissues.

During the summer both the organic nitrogen and the total reserve carbohydrate content are relatively constant, and there is only a minor drop at the beginning of October, when the total reserve carbohydrates increase very rapidly. In the dormant period during autumnal yellowing of the leaves, there is again a slight rise in total nitrogen until the end of December. That there is a migration of nitrogenous compounds from the leaves to the stem during autumnal yellowing has been demonstrated by Combes (1925), who made nitrogen determinations for the leaves and parts of the stem of green and yellowed specimens. The stems of the detached branches showed a greater increase of nitrogen than those left on the tree, and the lower leaves lost more than the upper. On a quantitative basis, Combes (1924) has shown with *Tilia, Acer, Fagus, Castanea,* and *Aesculus* that from one-half to two-thirds of the nitrogenous compounds in green leaves passes into the twigs during the normal yellowing. He also reported that no appreciable part is lost by leaching (rains and dew).

In spite of the fact that a considerable amount of nitrogen passes from the leaves into the twigs, there is no great gain in nitrogen on a dry weight basis. This may be accounted for in great measure by the proportionate increase in carbohydrates during the same period. That the nitrogen content remains constant or makes a slight gain during this period is evidence that the relative gain in nitrogen is proportionate to the gain in carbohydrates. On the basis of the entire twig, the same tendencies are shown as indicated for the complex tissues, but in amount of organic nitrogen on a dry weight basis, an intermediate position between that of the xylem and the periderm-cortex-phloem is maintained.

Amino and Non-amino Nitrogen

The amino acid content of the 2-3 year portions of apple twigs is exceedingly low, as shown in Table XI.

TABLE XI

REGIONAL AND SEASONAL DISTRIBUTION OF AMINO NITROGEN IN 2-3 YEAR PORTIONS OF APPLE TWIGS, MARCH 7, 1925, TO FEBRUARY 26, 1926

Expressed in per Cent Dry Weight

Date	Periderm	Cortex-phloem	Outer xylem	Inner xylem-pith	Entire twig
March 7	0.230	0.090	0.038	0.076	0.074
April 4	.296	.111	.059	.053	.085
May 16	.168	.133	.046	.085	.083
June 20	.286	.136	.038	.030	.071
September 17	.194	.109	.036	.036	.055
October 10	.221	.077	.045	.045	.065
October 23	.234	.077	.028	.063	.053
December 23	.231	.043	.031	.051	.052
February 26	0.111	0.078	0.019	0.034	0.041

According to this table and Figure 15, the percentage of amino-nitrogen in the periderm and cortex-phloem is usually higher than that in the xylem tissues. The amino-nitrogen content of the entire twig on a dry weight basis follows the trend of the outer xylem, but the amount is usually greater except during the first half of the dormant period.

The amino and non-amino nitrogen has been expressed as per cent of total organic nitrogen in Tables XII and XIII, and the upper two graphs of Figure 14.

These tables and the upper two graphs of Figure 14 show that amino nitrogen is relatively more abundant during the period of most rapid growth, May to July, and that non-amino nitrogen is relatively low during the same period. The non-amino nitrogen, however, is relatively more abundant during the dormant season, October to April, and amino nitrogen is relatively low during the same period. This is in harmony with the microchemical tests made by Kern (1923), who reports that protein substances are much more plentiful in winter in the cortex-phloem and parenchyma than during the summer season.

TABLE XII

REGIONAL AND SEASONAL DISTRIBUTION OF AMINO NITROGEN IN 2-3 YEAR PORTIONS OF APPLE TWIGS, MARCH 7, 1925, TO FEBRUARY 26, 1926

Expressed in per Cent of Total Nitrogen

Date	Periderm	Cortex-phloem	Outer xylem	Inner xylem-pith	Entire twig
March 7	24.73	7.86	10.27	23.03	13.96
April 4	28.46	8.76	16.86	12.92	14.40
May 16	26.66	19.85	25.72	42.50	26.77
June 20	45.40	26.24	54.28	61.43	41.76
September 17	29.92	18.47	32.72	27.69	25.00
October 10	35.08	17.22	35.38	41.06	29.54
October 23	35.04	11.16	18.33	37.06	20.38
December 23	34.47	5.51	15.50	28.33	16.25
February 26	15.00	10.68	10.55	18.88	12.81

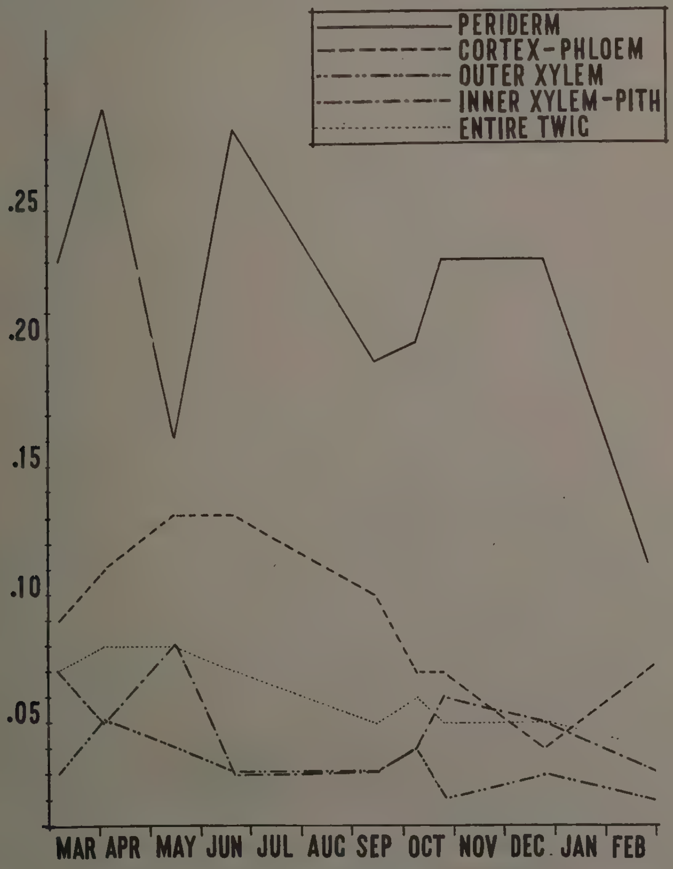

Fig. 15. Seasonal distribution of amino nitrogen in periderm, cortex-phloem, outer xylem, and inner xylem-pith. Expressed in per cent dry weight.

TABLE XIII

REGIONAL AND SEASONAL DISTRIBUTION OF NON-AMINO NITROGEN IN 2-3 YEAR PORTIONS OF APPLE TWIGS, MARCH 7, 1925, TO FEBRUARY 26, 1926

Expressed in per Cent of Total Nitrogen

Date	Periderm	Cortex-phloem	Outer xylem	Inner xylem-pith	Entire twig
March 7	75.27	92.14	89.73	76.97	86.04
April 4	71.54	91.24	83.14	87.08	85.60
May 16	73.34	80.15	74.28	57.50	73.23
June 20	54.60	73.76	45.72	38.57	58.24
September 17	70.08	81.53	67.28	72.31	75.00
October 10	64.92	82.78	64.62	58.94	70.46
October 23	64.96	88.84	81.67	62.94	79.62
December 23	65.53	94.49	84.50	71.67	83.75
February 26	85.00	89.32	89.45	81.12	87.19

REGIONAL AND SEASONAL DISTRIBUTION OF ASH

The apparent seasonal variation of ash in the complex tissues of the 2-3 year portions of apple twigs, is indicated in Table XIV and Figure 16.

TABLE XIV

REGIONAL AND SEASONAL DISTRIBUTION OF ASH IN 2-3 YEAR PORTIONS OF APPLE TWIGS, MARCH 7, 1925, TO FEBRUARY 26, 1926

Expressed in per Cent Dry Weight

Date	Periderm	Cortex-phloem	Outer xylem	Inner xylem-pith	Entire twig
March 7	2.51	6.88	0.61	0.60	1.84
		March 27*			
April 4	2.73	7.28	.61	.57	2.03
	April 18*				
May 16	2.53	7.67	.60	.51	2.13
	May 30*				
June 20	3.88	8.21	.62	.43	1.98
September 17	3.31	8.44	.49	.52	2.03
October 10	3.48	8.22	.59	.51	2.18
			October 4*		
October 23	3.42	6.46	.68	.69	1.73
	November 6*				
December 23	2.75	6.94	.66	.66	1.90
February 26	2.73	7.00	0.65	0.62	1.05

* Samples lost during ash analysis; figures for nearest available samples substituted with date indicated below.

The most striking fact brought out in Table XIV is the considerable difference in total ash content in periderm and cortex-phloem as contrasted with the xylem tissues. The cortex-phloem has the highest percentage, 6.46 to 8.44, followed by the periderm, 2.51 to 3.88. The woody tissues show only very slight variation. The total amount in each case is less than 1 per cent, 0.49 to 0.68 per cent (outer xylem) and 0.43 to 0.69 per cent (inner xylem-pith). The marked fluctuations in amount of ash in the cortex-phloem and periderm are probably only apparent. The curve for total carbohydrates in the case

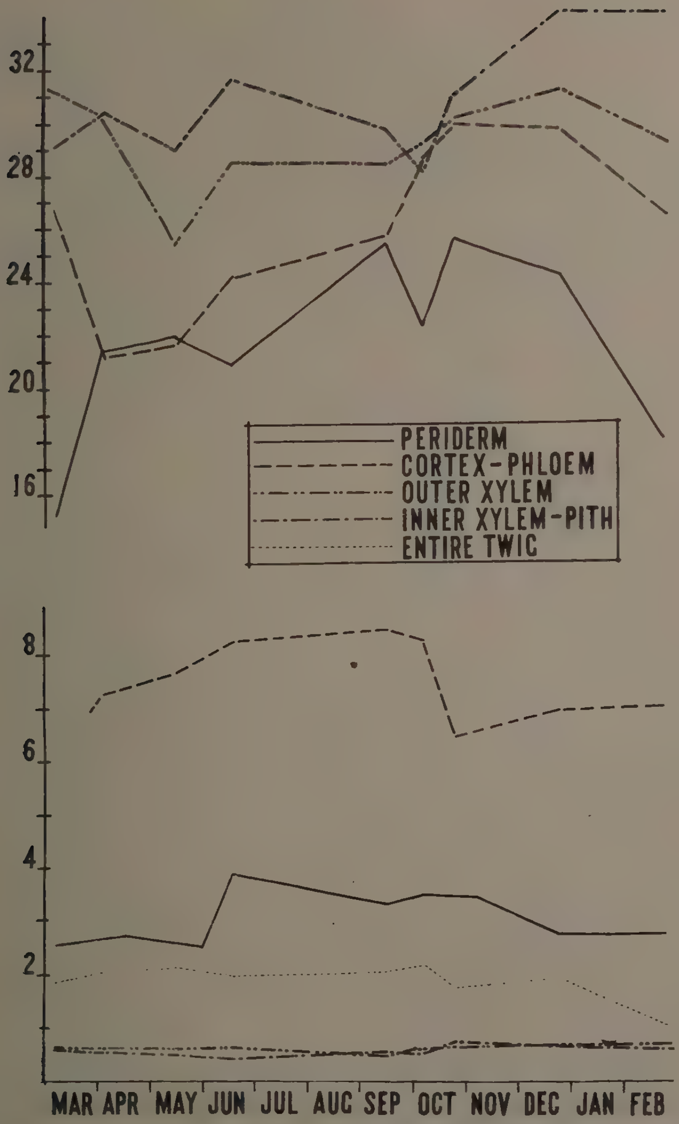

Fig. 16. Lower, seasonal and regional distribution of ash in periderm, cortex-phloem, outer xylem, inner xylem-pith, and entire twig. Expressed in per cent dry weight.

Upper, seasonal and regional distribution of total carbohydrates (except cellulose) in the four complex tissues—periderm, cortex-phloem, outer xylem, and inner xylem-pith. Expressed in per cent dry weight.

of the cortex-phloem is in some particulars the reverse of that for total ash; when the carbohydrates are relatively low during the growing season the ash content is highest, and when the reserve carbohydrates are translocated from the leaves to the twig at the time of leaf-fall, the ash is lowest. The same is, in general, true of the periderm. The fact that during the growing season both the ash and total reserve carbohydrates in the cortex-phloem show the same tendency indicates that the mineral matter is increased in proportion to the carbohydrates. The apparent decline of ash in the autumn is presumably the result of the relatively greater increase of total reserve carbohydrates, as shown in Figure 16. The ash content of the woody tissues is apparently quite constant, indicating that the ash constituents are increased in the same proportion as the carbohydrates.

When the ash content is expressed on the basis of the whole twig, the curve follows, in some particulars, that of the cortex-phloem, on a lesser scale.

Dormant Season

At the time of autumnal yellowing, part of the mineral constituents of the leaves is translocated to the stem. As early as 1878, Schröder demonstrated that potassium and phosphorus move back into the stem during the drying out of the leaves after freezing. Tucker and Tollens (1900) reported that the mineral elements in the leaves do not all pass to the twigs before leaf-fall, for rains and dews leach out a part.

Ramann (1912) pointed out that in frozen leaves the translocation of mineral constituents must take place in a short time between the thawing and drying of the frozen leaves. According to this authority, this may take place in a few hours.

The increase in mineral constituents in the twig due to the translocation of part of these elements from the leaves at the time of leaf-fall, is counterbalanced by the relatively great increase in total carbohydrates in the twig, so that in spite of the increase the percentage of ash on a dry weight basis shows an apparent decrease due to the relatively much greater proportion of carbohydrates. This is shown plainly for the periderm and cortex-phloem in Figure 16.

Migration of Mineral Constituents from Stem to Shoots and Leaves

The greater portion of the reserve mineral elements which have passed into the stem during normal autumnal yellowing is probably transported back to the expanding shoots in the spring together with mineral elements absorbed from the soil. Rippel (1923) reports that during the first spring growth of *Sambucus nigra* translocation of potassium and phosphorus from the stem to the young shoots and leaves is very marked.

PRACTICAL APPLICATIONS

Altho the primary aim of the research was to add to our scientific knowledge of apple physiology, the work was undertaken with a realization of the practical bearing of such contributions on horticultural research and practice. A better understanding of the functioning of the complex tissues of the apple twig is of immediate interest in the study of such problems as (1) the technic of sampling twigs, roots, etc.; (2) nutrition, (3) winter hardiness, and (4) translocation.

Analysis of Plant Organs

In the discussion of methods of procedure it has already been pointed out that the variation in the proportion of the various complex tissues during the season, due primarily to the difference in diameter of the organ, to changes of weight independent of volume, and to growth and senescence of tissues, puts the gross analysis of plant organs, twigs, spurs, roots, etc., on the defensive. The error from these sources should be fully realized when seasonal studies of plant organs are undertaken.

Nutrition

Since the appearance of the work of Kraus and Kraybill (1918) on the carbohydrate-nitrogen ratio as related to fruit bud formation in the tomato, it has been customary to extend this concept to apple physiology. The ratio has been variously expressed by different workers—sugar, starch, or total reserve carbohydrates over nitrogen. In order to test the validity of such a procedure with 2-3 year portions of apple twigs, the data have been expressed in these terms for the entire twig and for the four complex tissues, periderm, cortex-phloem, outer xylem, and inner xylem-pith, as shown in Table XV. The ratios are shown graphically in Figures 17, 18, 19, and 20.

In Figure 17 the ratios are shown on the basis of the entire twig. The acid-hydrolyzable hexosan–nitrogen, and the total carbohydrate–nitrogen ratios follow the same tendencies, but the latter is very much higher at all seasons of the year. The total sugar–nitrogen ratio follows a trend different from the preceding ratios from September to February.

Figure 18 shows that the total sugar–nitrogen ratio for all the four complex tissues is similar, with differences in magnitude during certain periods in the year.

The hydrolyzable hexosan–nitrogen ratio shows differences in trend for the woody tissues as contrasted with the periderm and cortex-phloem. Figure 19 shows that in the xylem tissues the decline from the summer maximum begins in June, but in the periderm and cortex-phloem there is a steady rise until September or October before a decline sets in.

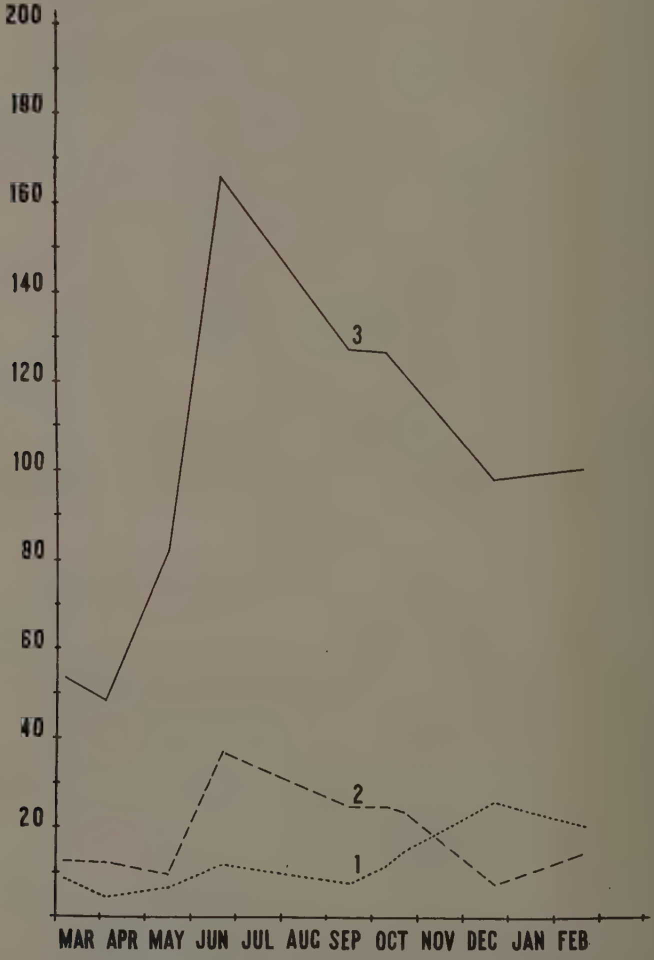

Fig. 17. Carbohydrate-nitrogen ratios; entire twig; total sugar-nitrogen ratio (1); acid-hydrolyzable hexosan-nitrogen ratio (2); and total carbohydrate-nitrogen ratio (3).

As shown in Figure 20, the total carbohydrate–nitrogen ratios show tendencies similar to those just described, but the ratios for the woody tissues are extremely high.

TABLE XV

Carbohydrate-Nitrogen Ratios: Periderm; Cortex-Phloem; Outer Xylem; Inner Xylem-Pith, and Whole Twigs; in 2-3 Year Portions of Apple Twigs

March 7, 1925, to February 26, 1926

Date	Periderm	Cortex-phloem	Outer xylem	Inner xylem-pith	Entire twig
Total Carbohydrates / Total Nitrogen					
March 7	16.24	23.21	84.02	88.00	53.56
April 4	20.58	16.76	86.71	78.92	48.28
May 16	34.79	32.19	141.33	144.95	81.80
June 20	33.22	46.32	407.14	632.80	165.70
September 17	39.07	49.34	257.45	222.07	126.77
October 10	35.26	59.26	223.30	256.00	126.09
October 23	38.07	43.33	200.33	181.41	119.76
December 23	36.94	38.05	155.45	183.94	97.31
February 26	24.17	36.09	159.16	183.83	91.75
Total Sugars / Total Nitrogen					
March 7	4.72	8.35	9.00	9.78	8.49
April 4	5.76	4.33	3.42	3.34	4.15
May 16	10.14	6.14	4.94	5.30	6.15
June 20	9.41	10.78	11.57	16.60	11.58
September 17	7.53	9.25	5.18	5.46	7.59
October 10	9.31	12.57	7.00	8.72	11.40
October 23	14.67	17.49	11.60	13.35	14.96
December 23	17.97	16.88	29.30	45.05	25.96
February 26	8.60	12.15	23.82	34.22	20.28
Acid-Hydrolyzable Hexosans / Total Nitrogen					
March 7	1.27	2.80	19.64	27.27	12.45
April 4	2.49	3.73	20.22	25.09	12.23
May 16	1.65	4.04	5.50	33.80	9.48
June 20	7.90	8.61	81.28	165.80	36.82
September 17	11.32	10.47	44.00	40.23	24.13
October 10	8.90	15.73	44.38	35.90	24.36
October 23	2.22	1.88	46.73	45.70	23.61
December 23	0.35	0.88	15.65	17.55	7.90
February 26	2.06	3.23	25.11	28.11	14.18

In all the cases considered above, the ratios for the entire twig follow the trend of the woody tissues as shown in Figures 18, 19, and 20. Apparently the results obtained by analyzing entire twigs would give values in most cases that approach the tendencies inherent in the xylem, the moisture transport, and the storage organ, since the trend in the cortex-phloem is not the same except in the total sugar–nitrogen ratios.

Winter Hardiness

Experiments by Beaumont and Hildreth (1927) and other workers have shown that there is a difference in the resistance of the various tissues of the terminal apple twig to low temperatures during the winter. In such researches the microchemical observations should be reinforced by macrochemical analyses whenever possible. By studying the complex tissues separately, a basis would be afforded for interpreting, if possible, the variability to cold resistance on a quantitative chemical basis.

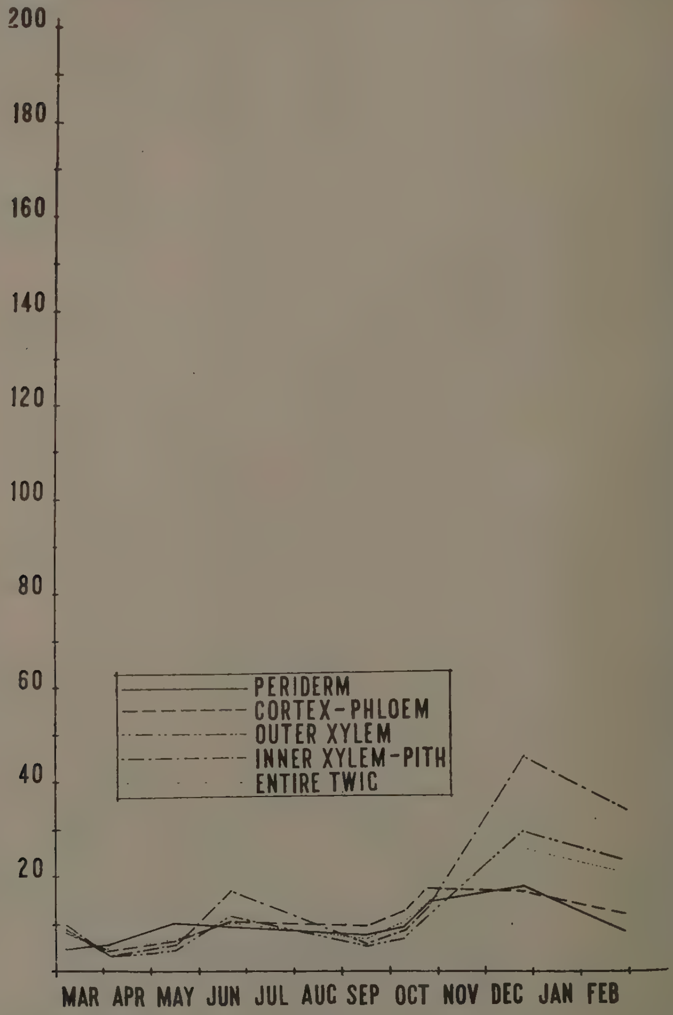

Fig. 18. Total sugar-nitrogen ratios; periderm, cortex-phloem, outer xylem, inner xylem-pith, and entire twig.

Translocation

In order to obtain an adequate conception of the translocation of materials in the tree as a basis for nutritional studies, the methods described should be extended to the entire tree—roots, trunk, branches, twigs, first-year shoots, buds, leaves, flowers, and fruits. The extent

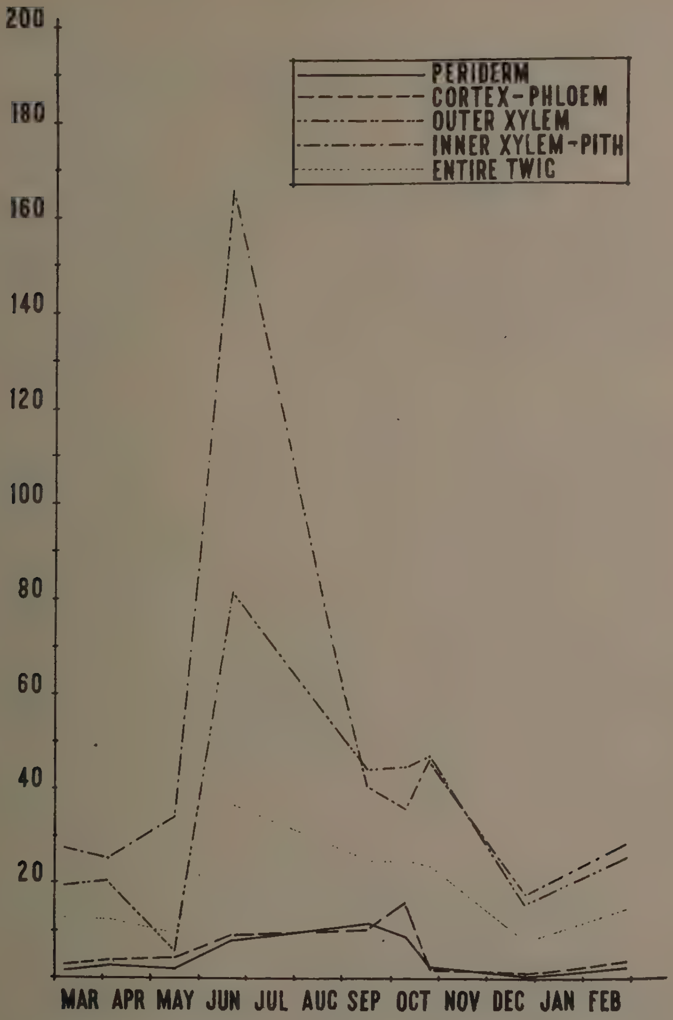

Fig. 19. Acid-hydrolyzable hexosan-nitrogen ratios; periderm, cortex-phloem, outer xylem, inner xylem-pith, and entire twig.

of the separation of the complex tissues would depend upon the nature of the organ, but the regional study should be made whenever practicable. For such a survey, 6-8 year trees, on their own roots, growing under the same conditions and with similar performance records, should be utilized. If possible, the experiments should be carried out on trees grown in tubs in the greenhouse under controlled temperature and moisture conditions. The data, when interpreted, would afford a much truer conception of the translocation of materials on a quantitative basis, and would reveal a dynamic picture of the functioning of the tree as a whole.

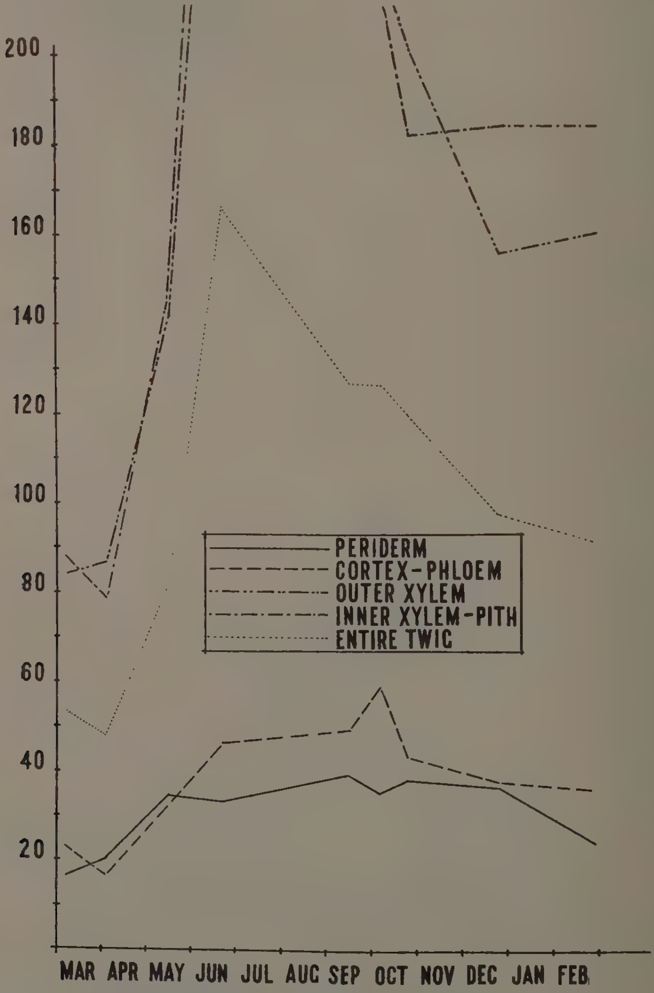

Fig. 20. Total carbohydrate-nitrogen ratios; periderm, cortex-phloem, outer xylem, inner xylem-pith, and entire twig.

CONCLUSIONS

The results presented and discussed in the preceding pages may now be summarized.

Methods

1. A method has been suggested for the separation of the complex tissues of woody plant stems for macrochemical analysis.

2. The macrochemical analysis of plant organs in seasonal studies has been put on the defensive. The error introduced by the difference in diameter of twigs and seasonal changes in absolute amount of dry matter independent of volume in the complex tissues, may be quite significant.

Moisture

3. In 2-3 year portions of apple twigs, the moisture content of the cortex-phloem is always highest and that of the periderm usually lowest. The two complex tissues, outer xylem and inner xylem-pith, follow the same general trend except that the percentage of moisture in the outer xylem shows a tendency to run higher at practically all times of the year. This is especially true during summer.

4. The summer moisture maximum in all the tissues was reached during the season of greatest precipitation, over 70 per cent.

5. The outer xylem apparently serves as the complex water-supplying tissue. The moisture content of this complex tissue follows the rainfall curve fairly closely. The complex tissues—periderm and cortex-phloem—seem to act independently of the total precipitation after a certain maximum has been reached, selecting the amount of water required from the common supplying tissues.

6. The drop in moisture of the periderm in June may be due to the differentiation of the phellem—with the cessation of life processes the moisture relations are those of dead suberized tissue.

7. On the basis of the entire twig, the individuality of the complex tissues naturally disappears and the tendency of the tissue in greatest relative abundance, outer xylem, is reflected.

8. The temporary decline in moisture content during the transition periods, March to April, and September to October, can not be adequately explained from the present data. It appears, however, that the moisture decline may be bound up with the chemical and physical changes of the protoplasm during the transition periods.

9. During the first part of the dormant period, October to December or January, there is a fairly marked decline in moisture content of all tissues. After this time until March, the moisture rises rapidly in the cortex-phloem and slightly in the inner xylem-pith, and declines slightly in the outer xylem. There is a continual decline in moisture content in the periderm during the entire period.

10. The trend in moisture content of the cortex-phloem and woody tissues is similar throughout the year, but the cortex-phloem is much more subject to marked fluctuations within the general trend, the outer xylem less so, and the inner xylem-pith least of all. The trend of the moisture content of the periderm departs from that of the other tissues in June to July.

11. From the end of December to the end of January, the moisture content of the complex tissues is not constant, but when the data are expressed on the basis of the entire twig the moisture content is practically constant.

Carbohydrates

12. On a dry weight basis, the total reserve carbohydrate content of the woody tissues is higher than that of the cortex-phloem at all times of the year, and that of the periderm is usually lower than that of the cortex-phloem.

13. The maximum in total reserve carbohydrates is reached in all the tissues after leaf-fall.

14. The pentosan content forms a relatively large proportion of the total reserve carbohydrates.

15. The fluctuations in pentosans at the beginning of the growing season are in great measure due to relative decreases in acid-hydrolyzable hexosans. Increases on a dry weight basis after leaf-fall disappear when expressed on the basis of per cent total reserve carbohydrates, showing that the pentosan content rises in proportion to the other reserve carbohydrates in the periderm and cortex-phloem. In the xylem tissues the increase in pentosans is relatively less than that of other reserve carbohydrates.

16. The acid-hydrolyzable hexosan content of the xylem tissues is usually greater than that of the periderm and cortex-phloem, and the latter reach a lower minimum than the former.

17. During the summer the acid-hydrolyzable hexosan content is built up in the periderm, cortex-phloem, and xylem tissues. In the xylem tissues there is a decline to a minimum in early October with a quick rise during the same month.

18. With the approach of cold weather there is a quantitative change of hexosans into sugar, beginning in September-October for the periderm and cortex-phloem and in October for the xylem tissues. The total sugars are also increased, owing to translocation from the leaves at time of autumnal yellowing.

19. There is a general depletion of hexosans in May in all the issues, owing to translocation of sugar used in growth extension.

20. In the periderm and cortex-phloem there are two hexosan naxima, September-October and March-April, and two hexosan minima,

December-January and May. In the xylem tissues there are apparently three hexosan maxima, October-November, March-April, and June; and three hexosan minima, September-October, December-January, and May.

21. During the winter minimum the hexosans disappear almost completely in the periderm and cortex-phloem, and are reduced more than 50 per cent in the xylem tissues. The value for sugars is twice as great as that of the hexosans at the minimum. This is not in agreement with the work of Alfred Fischer (1891). The difference in results is due to the technic used by Fischer, which gave him only a measure of the glucose in the vessels of the xylem.

22. The total sugar content of the periderm and cortex-phloem is always markedly higher than that of the xylem tissues.

23. All the tissues follow the same trend as far as total sugars are concerned.

24. During the winter the reducing sugar content of the periderm and cortex-phloem is higher than that of the non-reducing sugars, but this is reversed in the xylem tissues.

Nitrogen

25. The nitrogen content of the complex tissues of 2-3 year portions of apple twigs is extremely low, rarely rising above one per cent on a dry-weight basis in the periderm and cortex-phloem, and remaining below 0.5 per cent at all times in the outer xylem and inner xylem-pith.

26. As regards nitrogen content, the periderm, cortex-phloem, outer xylem, and inner xylem-pith follow the same trend throughout the year.

27. The nitrogen maximum is reached in March-April just preceding rapid growth extension.

28. After the marked decline in nitrogen with rapid growth extension, the nitrogen content is relatively constant during the summer.

29. From leaf-fall and through the winter the nitrogen content remains practically constant, with very slight downward or upward changes. This means that the nitrogen content increases in proportion to the carbohydrates in the fall, and the slight changes may be due to loss of combustible material by respiration or gain or loss in dry matter by translocation.

30. The amino-nitrogen content is highest during the growing season, decreases as the rest period approaches, and reaches a minimum during the dormant season.

31. The non-amino or protein nitrogen is highest during the dormant season, decreases as the active growing season approaches, and reaches a minimum in June.

32. The non-amino or protein nitrogen is consistently higher in the cortex-phloem than in the periderm and xylem tissues.

Ash

33. The amount of ash in the periderm, 2.51 to 3.48 per cent on a dry weight basis; cortex-phloem, 6.46 to 8.44 per cent, is higher than the mineral constituents in the xylem tissues, always below 0.7 per cent.

34. The fluctuations in ash content in the periderm and cortex-phloem may be misleading, and are apparently due to the relatively great fluctuations in total reserve carbohydrates. An apparent decline is indicated at the time a portion of the mineral constituents of the leaves is transported to the stem. This apparent decline is the result of the relatively greater increase of total reserve carbohydrates.

35. The ash content of the woody tissues is relatively constant, showing that the ash constituents are increased in proportion to the carbohydrates.

36. The increase of ash in cortex-phloem during the growing season shows the same tendency as the rise in total reserve carbohydrates, indicating that the mineral constituents are increased in proportion to the carbohydrates during this period.

SUMMARY

A method of separating the complex tissues of 2-3 year portions of apple twigs, periderm, cortex-phloem, outer-xylem, and inner xylem-pith, for the purpose of macrochemical analysis is described. The method may be applied to other plants.

The variation in the relative proportions of the different complex tissues during the season, owing to the difference in the diameter of the organ, to changes of weight independent of volume, and to the growth and senescence of tissues, points to the fact that in the gross analysis of plant organs—twigs, spurs, roots, etc.—in seasonal physiological studies, errors may be introduced which may minimize the usefulness of the results.

The seasonal macrochemical analysis of the four complex tissues of 2-3 year portions of apple twigs for moisture, carbohydrate, nitrogen, and ash fractions shows that the gross macrochemical analysis of plant organs (entire twigs) does not give a true picture for physiological studies. In most cases, when the data are expressed on the basis of the entire twig the tendency of one of the complex tissues, outer xylem, in greatest relative abundance, is reflected overshadowing the individuality of the other complex tissues. Accordingly, in seasonal macrochemical physiological studies, the complex tissues of the entire organ should be separately analyzed.

The seasonal changes in the moisture, carbohydrate, nitrogen, and ash fractions of four complex tissues, periderm, cortex-phloem, outer xylem, and inner xylem-pith are traced and the rôle of such changes in the normal physiology of the woody stem is discussed.

The application of the method described in the study of 2-3 year portions of apple twigs under central Minnesota conditions seems to indicate that the conclusions of Alfred Fischer (1891) regarding the "Stärkebäume" (starch-storing trees), do not hold for the apple variety studied. The increase in total sugars and a decline of acid-hydrolyzable hexosans, in both the cortex-phloem and the xylem tissues, with the approach of winter is apparently the outstanding fact from the standpoint of food storage during the dormant season. Such trees should more properly be designated as "Zuckerbäume" (sugar-storing trees).

The usefulness of the method described in the study of translocation, nutrition, and winter hardiness in plants is discussed.

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Agricultural Experiment Station

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LENGTH OF TRACHEIDS IN JACK PINE IN RELATION TO THEIR POSITION IN THE VERTICAL AND HORIZONTAL AXES OF THE TREE

By DAVID A. KRIBS

INTRODUCTION

It has long been known that the length of the tracheids of coniferous woods is influenced by the growing conditions and the environment of the individual trees. As far as the writer has been able to ascertain, however, no information is available regarding these relationships in *Pinus banksiana* Lam. (jack pine). The object of the investigation was to determine the relationship between length of the tracheids and their position vertically and horizontally in the axis of the tree; also to determine the variation in length of the tracheids in spring wood and summer wood.

The wood of jack pine resembles that of Norway and white pine, altho the lumber usually contains more knots, as the branches of jack pine are very persistent. The sapwood is white, the heartwood is pale brown. Trees under 50 years of age are composed mostly of sapwood. In trees from 60 to 100 years of age sapwood constitutes about 50 per cent of the volume. Growth rings vary from narrow to very wide, depending largely on growing conditions. The summer wood is dense and forms about 30 per cent of the volume of the annual ring. The transition from spring wood to summer wood is abrupt. According to Newlin and Wilson (14), the wood of jack pine shrinks 10.4 per cent in volume, 3.4 per cent radially, and 6.5 per cent tangentially, when the moisture content is reduced from green to oven-dry condition. The specific gravity of oven-dry jack pine wood based on the volume when green is 0.39. The air-dry wood contains about 12 per cent moisture and weighs approximately 30 pounds per cubic foot.

Microscopically, the structure of the wood resembles that of the other hard pines. According to Meyer (10), the rays constitute 8.10 per cent of the total volume. The size of jack pine tracheids has been studied by Penhallow (11), who found that spring wood tracheids are 34 microns across in a tangential direction and 52 microns across in a radial direction, while those of the summer wood measure 21 by 36 microns. The thickness of the cell wall in spring wood is 2.4 microns and in summer wood 6 microns.

HISTORICAL REVIEW

The length of tracheids in various species of wood has received little study. Sanio (12), in 1867, was probably the first investigator to publish results dealing with the length of tracheids. He found that in the cross-section of a stem or branch the tracheids increase in size for a certain number of annual rings from the pith until a maximum is reached, after which the size remains constant. He also found that tracheids in a given annual ring increase in size from the ground upward until a certain maximum is reached and then decrease in size toward the top. Sanio also states that there is no relation between the width of annual ring and the length of tracheid.

Shepard and Bailey (3), as a result of their study on white pine, Douglas fir, and spruce, agree with Sanio that no relationship exists between width of ring and length of tracheid, but disagree with him regarding the occurrence of a constant maximum tracheid length. The conclusions of Shepard and Bailey were confirmed by Miss Gerry (5, 6) and by Lee and Smith (7), altho these investigators claim that a greater growth in diameter may be correlated with a shorter tracheid.

Mell (9), working on the wood of black walnut, concludes that fast growing trees on deep black soil produce larger and longer wood fibers than trees that grow less rapidly on poorer soils. Likewise, MacMillan (8), in his work on red spruce, concludes that suppressed trees contain a higher percentage of short tracheids. Conversely, the wood of free grown trees contains a higher percentage of long tracheids.

MATERIALS AND METHODS

Seven trees of jack pine growing on the Cloquet Forest Experiment Station, Site I, were selected for the investigation. The trees were cut one foot above the ground. From each of the seven trees, cuts were made at intervals of 10 feet from the stump to the top.

Two trees were selected for the measurement of tracheids from spring and summer wood. From each section a block of wood about one-quarter of an inch square and one inch long was taken from the annual ring next to the pith and from every tenth ring from there out to the bark. In these two trees, the spring and the summer wood were carefully separated in each block. Small blocks were cut from the other five trees in a similar manner, but no attention was paid to the separation of the spring and the summer wood.

Method of Macerating the Tracheids

Each small block was cut into pieces about one millimeter in cross-section and 10 millimeters in length. These pieces were put into test tubes containing 10 cc. of a 50 per cent solution of nitric acid to which was added 0.3 gram of potassium chlorate. The test tubes and contents were then submerged in boiling water for from 8 to 10 minutes. If cooked longer than this, some of the tracheids were broken down. At the expiration of 10 minutes the test tubes were removed from the boiling water and the tracheids were washed with a small quantity of tap water.

Method of Measuring the Tracheids

The tracheids were measured as soon as possible after maceration. A projection method was used, employing a lantern with a 400-watt lamp, triple condensers, and water cell. The light was projected through a microscope fitted with a 48 millimeter objective and a 10x ocular.

About 100 tracheids were transferred from the bottle to a clean glass slide by means of a dropper. The excess water was absorbed and a few drops of glycerine were added, after which a cover glass was put on. The image was projected from a prism through a light-tight box on a sheet of paper. The perfect tracheids were then drawn on the paper, the ends being carefully marked.

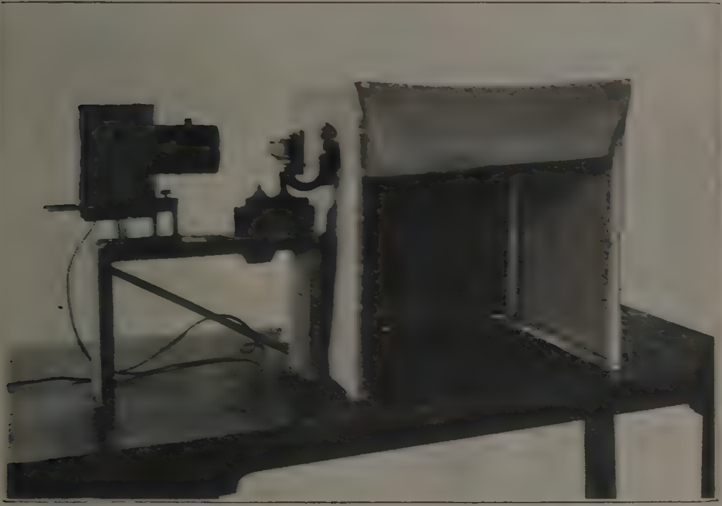

Fig. 1. Apparatus Used in Determining the Length of Tracheids

The slide was so moved about on the stage of the microscope that measurements were not duplicated. After the tracheids were projected and drawn, a millimeter scale was projected, using the same magnification. This scale was transferred to flexible aluminum tape and checked for accuracy. A total of 12,500 tracheids were drawn on paper and measured directly in millimeters.

EXPERIMENTAL RESULTS

The data from the seven trees were averaged together by sections. The data for each section were plotted as separate curves, using the length of the tracheids in millimeters as the ordinate and the age of the tree in years as the abscissa. The tracheid length for each age class in the individual curves was replotted, replacing age of tree in years by height above ground in feet as the abscissa. This procedure resulted in the curves shown in Figure 2, which indicate the relation between the length of the tracheids and their position in the vertical axis of the tree.

The curves in Figure 3 were constructed by replotting the values from the smoothed curves in Figure 2. The values given in Table I were taken directly from the curves in Figure 3, the tracheid lengths being taken at five-year intervals. Table I shows that in the annual ring next to the pith the tracheids increase in length rapidly from the base to the section at 21 feet above the ground, after which the length remains practically constant to the top of the tree. From the first annual ring to the 40th, the tracheids increase in length to the section at 41 feet above the ground, then decrease in length to the top. From the 45th to the 80th annual ring, the tracheids increase in length to the section at 31 feet above the ground, then remain practically constant or increase slightly in length to the top.

TABLE I

Relation of Age and Position in Vertical Axis to Length of Tracheids

Length of Tracheids in Millimeters

(Data from Curves in Figure 3)

Age, years	Height above ground, feet						
	1	11	21	31	41	51	61
1	1.10	1.20	1.35	1.40	1.42	1.40	1.45
5	1.75	2.00	2.20	2.40	2.45	2.25	2.10
10	2.15	2.50	2.75	2.95	2.90	2.75	2.60
15	2.40	2.95	3.20	3.25	3.25	3.05	2.93
20	2.58	3.20	3.45	3.50	3.50	3.30	3.20
25	2.75	3.40	3.60	3.70	3.70	3.55	3.40
30	2.86	3.50	3.80	3.85	3.85	3.72	3.62
35	2.96	3.65	3.90	3.98	3.98	3.90	3.80
40	3.08	3.75	4.00	4.08	4.10	4.05	4.00
45	3.15	3.80	4.08	4.16	4.20	4.25	4.25
50	3.22	3.85	4.15	4.25	4.25	4.35	4.45
55	3.25	3.88	4.20	4.30	4.32	4.45	4.50
60	3.25	3.90	4.24	4.32	4.35	4.50	4.50
65	3.30	3.92	4.25	4.35	4.40		
70	3.30	3.92	4.25	4.35	4.40		
75	3.30	3.95	4.30	4.40	4.45		
80	3.30	3.95	4.30	4.45			
85	3.30						

An analysis of the data given in Figure 3 and Table I indicates that the tracheids in the cross-sections at 1 foot, 11 feet, 21 feet, 31 feet, and 41 feet above the ground increase rapidly in length with the age of the tree up to about 40 years, after which the length increases slightly or remains constant to the bark. The tracheids in the sections 51 and 61 feet above the ground increase in length rapidly with the age of the tree from the pith to the bark. The curves at 41, 51, and 61 feet above the ground are more linear than those representing the other cross-sections. A biometrical study of the data in question confirms this conclusion. It is also evident that the longest tracheids are found in the rings from the 50th to the bark in the higher parts of the trunk, or from the section 31 feet above the ground to the top of the tree, and that the maximum lengths are found near the bark in the cross-section at 51 and 61 feet above the ground.

Table II shows the average maximum and minimum tracheid lengths for all trees. The table was prepared by averaging the maxima and minima in each section of the seven trees.

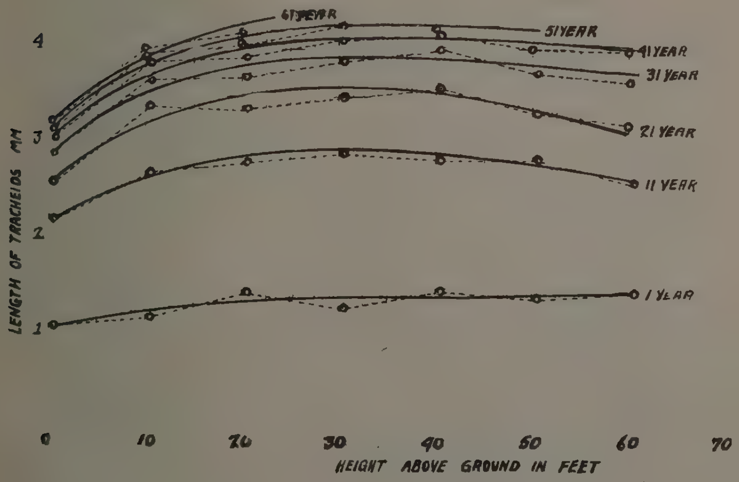

Fig. 2. Relation of Length of Tracheids and Their Position in Vertical Axis of Tree

Table II shows the same relations given in Table I. It is evident from Table II that the average maximum tracheid length is 5.05 millimeters; the average 3.20, and the minimum, 0.75.

In Table III are given the results obtained by averaging the length of the spring and the summer wood tracheids for each section in two trees. Altho there are a few apparent exceptions, the summer wood tracheids are somewhat longer than those of the spring wood.

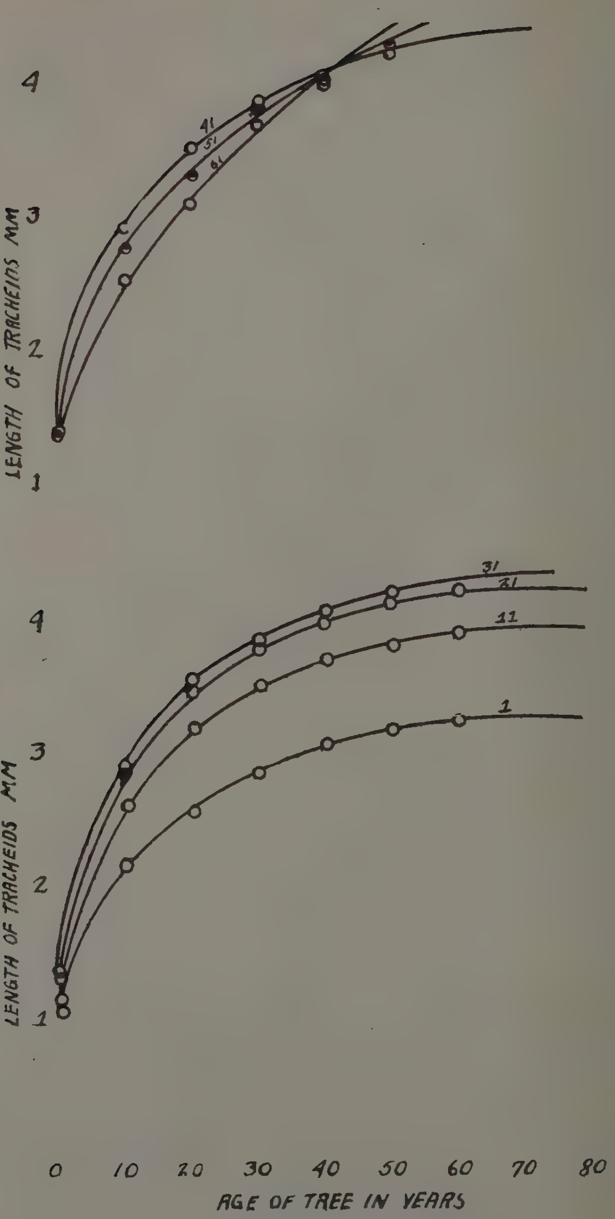

Fig. 3. Relation of Age to Length of Tracheids at the Cross-Sections 1, 11, 21, 31, 41, 51, and 61 Feet Above Ground

TABLE II

Maximum and Minimum Tracheid Length Showing Effect of Age and Position in Vertical Axis on Length of Tracheids

Length of Tracheids in Millimeters

Years	Section 1		Section 2		Section 3		Section 4		Section 5		Section 6		Section 7	
	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min
1	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
11	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
21	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	4.19	3.86	4.44	4.06	4.06	[illegible]	[illegible]	[illegible]
31	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	4.75	3.14	4.74	4.00	4.50	[illegible]	[illegible]	[illegible]
41	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	4.95	3.50	4.80	3.41	4.70	3.30		
51	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	4.91	3.80	4.80	3.34				
61	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]								
71	3.78	3.44	5.00											
81	3.97	3.70												

TABLE III

Mean Tracheid Length, Spring Wood and Summer Wood for Two Trees Showing Effect of Age and Position in Vertical Axis on Length of Tracheids

Length of Tracheids in Millimeters

Years	Section 1		Section 2		Section 3		Section 4		Section 5		Section 6		Section 7	
	Early wood	Late wood	Early wood	Late wood	Early wood	Late wood	Early wood	Late wood	Early wood	Late wood	Early wood	Late wood	Early wood	Late wood
11	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
21	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
31	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]		
41	[illegible]	[illegible]	[illegible]	[illegible]	3.79	[illegible]	4.00	4.38	[illegible]	[illegible]	[illegible]	[illegible]		
51	3.14	3.16	4.14	4.07	4.10	4.16	4.44	4.30						
61	3.40	3.44	4.47	4.51	4.14	4.17								
71	3.74	3.78	4.46	4.30										

It seemed desirable to test the reliability of certain of the relationships that have been brought out above by the calculation of biometric constants for two of the trees.[1]

The standard deviations for both age of tree and length of tracheids for each section in the two trees are necessary for the determination of the correlation coefficient, r, measuring the relationship between the age of the tracheids and their length. These are shown in Column 1, Tables IV and V, respectively.

The correlation coefficient measuring the relationship between age and tracheid length for each section in the two trees appears in Column 2, Tables IV and V.

These are substantial values and unquestionably significant. As the plotting of the mean tracheid lengths for each cross-section, as shown in Figure 3, indicated that a straight line relationship between length of tracheid and age does not exist, the correlation ratio, η, between age and tracheid length was determined for each cross-section in the two trees and is given in Column 3, Tables IV and V.

TABLE IV

STANDARD DEVIATION, CORRELATION COEFFICIENT, CORRELATION RATIO, AND BLAKEMAN'S CRITERION FOR EACH SECTION IN TREE F

Section	I		II	III	IV
	Standard deviation		Correlation coefficient	Correlation ratio	Blakeman's criterion
	Length of tracheid	Age of tree, years			
1	0.8003	23.1054	0.5152	0.9390	16.90
2	0.9880	20.8865	.6931	.9463	10.38
3	0.8368	19.7877	.5492	.8826	12.79
4	1.2013	17.8302	.8139	.9456	6.53
5	1.0575	16.3682	.7166	.9283	8.57
6	0.9768	13.3207	.8352	.9207	4.70
7	0.9500	9.3140	0.9066	0.9413	2.68

TABLE V

STANDARD DEVIATION, CORRELATION COEFFICIENT, CORRELATION RATIO, AND BLAKEMAN'S CRITERION FOR EACH SECTION IN TREE G

Section	I		II	III	IV
	Standard deviation		Correlation coefficient	Correlation ratio	Blakeman's criterion
	Length of tracheid	Age of tree, years			
1	0.7976	25.8199	0.8212	0.9558	8.10
2	1.0658	22.9129	.8557	.9569	6.57
3	1,0606	21.1168	.8464	.9636	6.64
4	1.0149	19 3750	.8471	.9734	6.92
5	0.9655	17.0782	.8779	.9724	5.52
6	0.9926	14.1421	.9027	.9704	4.24
7	0.7385	11.1803	0.9507	0.9580	1.24

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[1] Thanks are due to Dr. J. Arthur Harris, of the Department of Botany, for help in this phase of the work.

As η is the ratio of the standard deviation of the weighted means of arrays of tracheid length to the standard deviation of tracheid length in the whole series, it is always positive. The value of η is independent of the form of the distribution of the means of y, where y represents the length of the tracheids. It is therefore valid whether the mean exhibits a straight or a curved line relationship to age.

The correlation ratio is high for each section. In both trees it is of the order $\eta = 0.95$. This shows that the deviation of tracheid length from the regression curve will be relatively small. Estimates read from such curves will therefore represent a relatively high degree of accuracy.

At a distance of one foot above the ground the difference between the correlation ratio, η, and the correlation coefficient, r, is very large. In successively higher sections the correlation ratio and the correlation coefficient approach each other until they become nearly identical in that section when near the top of the tree.

As the correlation coefficient, r, and the correlation ratio, η, approach each other in successively higher cross-sections, the regression line for these sections appears to be changing form. In order to test this assumption, Blakeman's (4) criterion of linearity of regression was employed. This is a formula involving both the correlation coefficient, r, and the correlation ratio, η. If the criterion

$$\frac{\zeta}{E_{\zeta}} = \frac{\sqrt{N}}{.67449} \cdot \frac{1}{2}\sqrt{\zeta} \cdot \frac{1}{\sqrt{1 + (1-\eta^2)^2 - (1-r^2)^2}}$$

where

$$\zeta = \eta^2 - r^2$$

is less than 2.5, the regression is linear; if greater than 2.5, it is probably significantly non-linear.

The application of Blakeman's test to both trees showed a large value for the criterion at the base of the tree, which gradually became smaller at higher levels, as shown in Tables IV and V, Column 4.

As the correlation coefficient, r, rapidly approaches the correlation ratio, η, in passing from the base to the top of the tree, and as the values of Blakeman's criterion diminish rapidly from the base to the top, it is clear that for each successively higher cross-section from the base to the top of the tree there is a closer approach to a linear relationship between tracheid length and age of tree, or that the increase in the length of the tracheid is more directly proportional to age.

DISCUSSION AND CONCLUSIONS

The results of this investigation are in harmony with those obtained by other investigators, in that it was found that tracheids increase in length from the base of the tree upward until a certain maximum length is reached and then decrease in length to the top of the tree.

On the other hand, it is found that in jack pine the length of the tracheids in the annual ring next to the pith remains constant after this maximum is reached and that the length of tracheids in the rings from the 45th to the bark either remains practically constant or slightly increases to the top of the tree.

These results agree with those obtained by Shepard and Bailey (3) in connection with their study of the variations in length of coniferous tracheids, in that, in the rings near the bark, the maximum tracheid length occurs in the higher parts of the tree.

The results of this study partly agree with those of other investigators, in so far as it was found that the tracheids increase in length rapidly up to a certain maximum with age, after which, as Shepard and Bailey (3) point out, there is a marked decrease for ten years, then an increase. According to Lee and Smith (7), there are comparatively small irregular increases or decreases in tracheid length with a slight average increase toward the periphery. The results of this investigation show that after this maximum length is reached, the tracheid length remains constant or increases slightly to the bark for the cross-sections in the lower part of the tree and increase rapidly in length from the pith to the bark in the higher parts of the tree. The results also agree with those of Lee and Smith (7) in that they show the summer wood tracheids to be slightly longer than those of the spring wood.

A result brought out in this investigation that has not been mentioned by previous workers, is that from the base to the top of the tree each successively higher cross-section shows a greater degree of linear correlation between age and tracheid length. This fact is clearly shown in Tables IV and V. A possible explanation of this fact is that the tree in the sapling stage has a small crown, small trunk, few branches, and a comparatively small root system. Each year added to the life of the tree increases the development of the crown, trunk, branches, etc. It is conceivable that the younger tracheids near the top or in the crown of the tree have a greater reserve food supply to draw on than the corresponding tracheids had when the tree was in the sapling stage.

It is claimed by Bailey (1) that the size of the cells in the secondary xylem is determined by the size of the cambium initials and also by changes that take place in their derivative cells during differentiation into tracheary elements. He also points out that the cambial initials of conifers increase rapidly in length up to about 100 years of age and then remain constant, and that by allowing for a 5 to 10 per cent error it is possible to use the tracheids of gymnosperms as indices of the approximate length of the cambial initials.

According to Bailey (2) the anticlinal divisions in non-stratified meristems are pseudo-transverse, the fusiform initials elongate, sliding by one another, until they attain a certain size. They then divide by means of a more or less oblique partition into two short halves which in turn elongate and divide. Owing to the fact that the cells do not divide and elongate in unison, there is a considerable variability in the length of adjacent initials.

It seems to the writer that the whole problem of tracheid growth depends upon three important factors—the frequency of cell division, the amount of elongation before division, and the amount of elongation of the daughter cells. Therefore, if such growth factors as quality of soil, moisture conditions, and light requirements could be correlated with the above factors, the cause of the difference in tracheid lengths might be determined.

SUMMARY

1. The results of measuring 12,500 tracheids in seven trees show that the maximum tracheid length in jack pine is 5.05 mm., the average 3.20 mm., and the minimum 0.75 mm.

2. From the base to the top of the tree each successively higher cross-section shows a greater degree of linear correlation between age and tracheid length.

3. For the annual ring next to the pith, the tracheids increase in length rapidly from the base to the section at 21 feet above the ground, after which the length remains practically constant.

4. From the first annual ring to the 40th, the tracheids increase in length to the section at 41 feet above the ground, then decrease in length to the top.

5. From the 45th to the 80th annual ring, the tracheids increase in length to the section at 31 feet above the ground, then remain practically constant or increase slightly to the top.

6. The tracheids in the cross-sections at 1 foot, 11 feet, 21 feet, 31 feet, and 41 feet above the ground rapidly increase in length with age of tree to about 41 years, after which they increase slightly or remain constant to the bark.

7. The tracheids in the sections 51 and 61 feet above the ground increase in length rapidly from the pith to the bark.

8. The longest tracheids are found in the rings from the 50th to the bark in the higher parts of the tree, or from the cross-section at 31 feet above the ground to the top.

9. Maximum tracheid lengths are found near the bark at the cross-section 51 feet above the ground to the top of the tree.

10. The maxima and minima tracheid lengths behave similarly to the average in the relation of age and position in the vertical axis to length of tracheids.

11. The tracheids of summer wood are slightly longer than those of spring wood.

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The Agricultural Credit Situation in Minnesota

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CONTENTS

Page

Introduction 5

Mortgage encumbrance 8

  Situation in 1925 9

  Survey data 11

  Changes since 1890 17

  The farm owner's equity 19

  Movements in land prices 21

  Changes in size and number of farms 24

  Changes in tenancy 26

  The "agricultural ladder" 26

  Tenancy in relation to the credit problem 30

  Mortgage encumbrance in Minnesota as compared with that of other states 31

  Distribution of mortgage indebtedness within the state 32

  Geographic comparison of mortgage encumbrance and tenancy combined.. 34

  Progress of individual farmers 36

  Sources of long-term loans 39

  Second mortgage loans 46

  Mortgage interest rates 48

Short-term credit 52

  Purpose of short-term loans 54

  Security 55

  Need for better bank loan practices 55

  Period of collateral or personal loans 56

  Mercantile credit 57

  Short-term credit in cut-over areas 61

Intermediate credit 62

  Volume of business of intermediate credit banks 64

    Agriculutral credit corporations—Minnesota 66

The problem of the local bank 68

  Banks have not stood the test 69

  Why banks have failed 71

    Failures due to too small banks and too many 73

    Failures due to agricultural loans 74

    Failures due to bad management 79

    "Frozen assets" 84

  Banking regulation as a means of improvement 84

  Changes in banking laws 86

    Further changes proposed 88

Bibliography 91

Appendix 94

ILLUSTRATIONS

Page

Fig. 1. Mortgaged owner-operated farms in the United States 8
2. Relation of land prices to other price levels, basis 1910 conditions 21
3. Relation of land prices to commodity price levels, basis 1890 conditions 22
4. Increase of mortgage indebtedness with value of farms, by counties, 1925 25
5. Percentage of tenancy in each age group for farm census years from 1890 to 1920 for Minnesota 28
6. Increase in laborers and tenants, 1890 to 1910 29
7. Percentage of owner farms encumbered and ratio of debt to value of full owner mortgaged farms, by sections, 1925 31
8. Changes in percentage of tenancy 1880 to 1925 35
9. Distribution of agricultural credit corporations and national farm loan associations in Minnesota, April 1, 1926 47
10. Mortgage interest rate, 1920, by counties 48
11. Mortgage interest rates in 1890 and 1920 by crop reporting districts .. 49
12. Interest rates, 1895 to 1924 51
13. Short term interest rates in Minnesota by crop reporting districts, 1916 59
14. Bank deposits per capita in 1912 and 1920 68
15. Number of banks per million dollars of deposits and percentage of banks failing between 1920 and Dec. 31, 1925 75
16. Bank loans and bank failures in the United States 76
17. Location of state bank failures, 1920 to 1926, inclusive 77
18. Relationship of wholesale prices of agricultural and non-agricultural products 79
19. Changes in savings accounts, time certificates, and checking accounts for Minnesota state banks 80
20. Commercial state and national banks in Minnesota 83

THE AGRICULTURAL CREDIT SITUATION IN MINNESOTA

B. M. GILE and J. D. BLACK

INTRODUCTION

The 1925 agricultural census, as of January 1 of that year, reported 48.6 per cent of the full-owner and part-owner operated farms of Minnesota as having a mortgage encumbrance—a decrease of 3.8 per cent from the 52.4 per cent reported mortgaged in 1920. For the 1920 census, 6.9 per cent of the owner operators did not state whether their farms were mortgaged, as contrasted with only 0.8 per cent for the 1910 census. Possibly a still larger percentage did not report on this question in 1925 and a large majority of those not reporting may have had mortgages on their farms. The mortgages reported on owner-operated farms in 1925 averaged $5,117, or 43.6 per cent of the owners' estimated values. On January 1, 1920, the average mortgage amounted to $4,419, or 27.5 per cent of the estimated values of the farms mortgaged. There was thus an increase of $698 in the average size of the mortgages, and of 16.1 per cent in the ratio of debt to value of farms mortgaged.

In the same period, the number of rented farms increased from 44,138 to 51,081, or from 24.7 per cent to 27.1 per cent of the total number of farms in Minnesota.

Combining mortgage encumbrances with tenancy on a value basis, gives results as follows:

	1920	1925
Value of all farms in Minnesota	$3,301,168,325	$2,393,741,745
Value of rented farms	1,059,182,613	801,226,969
Value of mortgages on full-owner farms	254,475,222	267,026,995
Value of mortgages on part-owner farms[1]	59,822,000	80,042,000
Value of managed farms	50,234,658	19,930,059
Total values not owned by owner operators	1,877,453,840	1,225,515,740
Per cent of value of farms in Minnesota not owned by operators	43.1	48.8
Per cent of value of farms in Minnesota owned by operators[2]	56.9	51.2

Thus the farmers of Minnesota, on January 1, 1925, owned only 51.2 per cent of the estimated value of the farms in the state. The comparable figure for 1920 was 56.9 per cent, which indicates a decline from 1920 to 1925 of 5.7 per cent.

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[1] Estimated on the basis of percentage of full-owner operated farms mortgaged. There may be an error in this; but it ought not seriously to affect the comparability of the results between census periods.

[2] This does not include the value of farm mortgages that farm operators may hold against other farms, or the value of other farms that they own and rent to others.

In 1910, only 46.0 per cent of the owner-operated farms in Minnesota were mortgaged, and the mortgages averaged only $1,864 per farm—26.4 per cent of the estimated value of mortgaged farms. The operators of Minnesota farms at that time owned 65.5 per cent of the value of the farms in the state. The comparable figure for 1900, however, is only 52.5 per cent and for 1890, only 52.0 per cent. Thus the percentage of the farm values owned by the operators of farms increased considerably from 1900 to 1910, but since 1910 the situation has reversed and a larger and larger percentage of the values of Minnesota farms has passed out of the hands of the operators into the hands of the landlords, mortgage holders, and employers of managers, until the percentage owned by them in 1925 was about the same as in 1890.

Between 1920 and 1925, there were 1,378 farm bankruptcies in Minnesota, as compared with 337 between 1910 and 1920. A comparison of bankruptcies among farmers in Minnesota and in neighboring states is shown in Table I.

TABLE I

Bankruptcy Among Farmers, 1910 to 1925

State	1910 to 1919	1920 to 1925
Minnesota	337	1,378
North Dakota	718	2,406
South Dakota	249	816
Montana	463	1,737
Iowa	690	2,492
Wisconsin	78	522
Illinois	409	697

In all states there have been considerably more bankruptcies in the last 6 years than in the preceding 10 years. No doubt a majority of the farmers that lose their farms give them up without going through bankruptcy, either by letting their contracts go by default or by giving a deed to the holder of the mortgage. The proportion of failures going through bankruptcy has increased greatly in late years, so that the above figures exaggerate the change.

The agricultural census of January 1, 1925, included a question asking for "the total amount of other debts which you owe, not secured by mortgages on real estate." But the Census Bureau has not tabulated the answers.

A special survey of 240 farms made in Minnesota in the fall of 1924, just before the census was taken, showed an average non-mortgage indebtedness of $694 per owner-operator and $1,147 per tenant.

The year 1924 was the best Minnesota farmers had had since 1919.[3] No doubt some debts had already been paid off that year. The $694 of non-mortgage indebtedness of owner-operators consisted of personal and collateral loans and store credit. The latter was 27.2 per cent of the total. The $1,147 of indebtedness of the tenant-operators was 14.7 per cent store credit.

In a survey of 157 farm families in the fall of 1925, Carle C. Zimmerman, of the University of Minnesota, found that the average interest of borrowed funds amounted to $260. This survey covered seven communities. The lowest average amount of interest paid per farm in any community was $68 and the highest, $620, in the Blackduck (Beltrami County) and Tyler (Lincoln County) communities, respectively. The average paid on mortgage debt during the year was $172, with a minimum per farm of $11 in the Blackduck area, and a maximum of $353 in the Zumbrota area (Goodhue County). The average amount paid on all other indebtedness, not including insurance, was $109, with a minimum by communities of $41 and a maximum of $231. The average amount paid on all indebtedness other than insurance was $281, which was only slightly more than the $260 paid out for interest on borrowed funds.

Another survey made by Dr. Zimmerman in 1926, in the vicinity of Benson, Crookston, Litchfield, Mora, Spring Valley, and Tracy, included 215 owners and 120 tenants. The average interest paid during the previous year amounted to $334 per owner, or $454 per indebted owner. The Tracy area (Lyons County) averaged the highest per indebted owner and the Mora area (Kanabec County) the lowest. These areas paid respectively $779 and $176. The tenants averaged $89 of interest paid, or $99 per interest-paying tenant. The owners had reduced the average indebtedness on their farms $147 during the year and their other indebtedness $44. Tenants had no payments to make on the farms they were operating but made payments on non-mortgage indebtedness amounting to $91. Both owners and tenants in this 1926 survey were expending annually more of their income to pay interest bills than for debt reduction.

The foregoing data present a situation that needs very careful consideration. Involved in it are elements that are at the very foundation of our rural civilization. It is the purpose of this bulletin to uncover as many as possible of the real facts as to this situation, discover their significance and their causes, and show their relation to the credit institutions that have been established and to their manner of functioning.

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[3] A rough index of gross incomes for Minnesota farmers in recent years runs about as follows: 1919, 234; 1920, 160; 1921, 109; 1922, 130; 1923, 149; 1924, 181; 1925, 181; and 1926, 188. The comparable net incomes run as follows: 232, 149, 86, 109, 121, 177, 202, and 210.

While the study was of Minnesota conditions, its findings will no doubt apply in large measure to many other states.

MORTGAGE ENCUMBRANCE

The mortgage encumbrance of farms is important from the standpoint of credit, because in terms of dollars it represents by far the largest use made of credit in agriculture. To understand long-term credit for agriculture, we must analyze carefully the conditions determining mortgage encumbrance.

The principal data available concerning mortgage encumbrance are those collected each ten years by the Census bureau, and those collected in the special farm census of January 1, 1925. In the 1920 and the 1925 censuses a mortgage was defined to include "all debts secured by instruments locally called 'mortgages'; also all debts represented by judgment notes, confessions of judgments, deeds of trust, deeds with vendor or lien clause, bonds, or contracts for title, or any other legal instruments (other than mechanics' liens or crop liens) that partake of the nature of mortgages upon real estate."[4] Mortgage encumbrance thus includes the so-called "land contracts" under which, in Minnesota, considerable land is sold to young farmers. Generally speaking, a farmer selling his farm asks for a cash payment amounting to at least half the sale price, but there is a pronounced tendency to extend this limit to two-thirds. Also, many farms are sold on a con-

MORTGAGED OWNER-OPERATED FARMS IN UNITED STATES

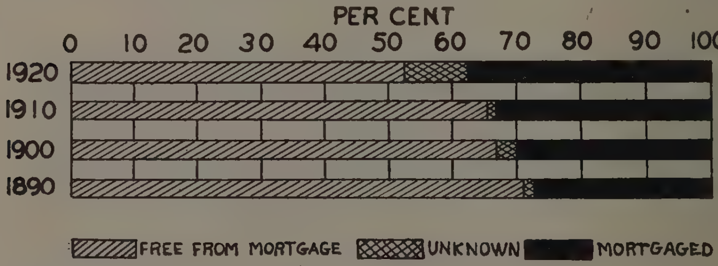

Fig. 1. The mortgaged farms in the United States increased about 9 per cent between 1890 and 1920. The 1925 agricultural census shows that between 1920 and 1925 mortgaged farms declined nearly 2 per cent. "Unknown" farms are those whose debt status was not reported. Preliminary reports of the 1925 census do not show how many farms failed to report on mortgage debt.

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[4] Census 1920, Vol. VI, Part I, p. 479.

tract for deed with the buyer paying down in some cases less than a third of the purchase price.[5]

Situation in 1925

To understand the mortgage situation in Minnesota in 1925, as presented in earlier paragraphs, it must be considered in relation to the other facts presented in Table II. According to these facts, the actual number of mortgaged owner-operated farms decreased over 3000 between 1920 and 1925, in spite of the fact that the total number of farms in the state increased nearly 10,000 in the same period. In terms of percentage, only 48.6 per cent of the owner-operated farms were mortgaged in 1925, as compared with 52.4 per cent in 1920. This is an unexpected development, quite contrary to prevailing impressions. One is inclined to doubt the authenticity of the census figures. There was, however, a similar development in North Dakota, Montana, Wisconsin, Illinois, and some other states (Table III). For the whole group of west north central states, there was a decrease of 0.6 per cent in the number of owner-operated farms mortgaged. A part explantion is the increase of nearly 7,000 in rented farms and of 3,600 in part-owner farmers in Minnesota during this period. This no doubt represents, in part, a substitution of landlord ownership for mortgaged-operator ownership. Many heavily mortgaged farms no doubt reverted to their former owners or passed into the hands of mortgage holders, who are far less likely to have mortgages against them than their "shoe-string" operators. Any foreclosure or its equivalent is likely to work out in this way. No doubt the decrease in the average size of farms from 169 to 160 acres in this period and especially in the value per acre from $109 to $79, has made it possible for more persons to own them without mortgages. The lower land values are, other things being the same, the lower the proportion of farms likely to be mortgaged. (See Fig. 4.) This is just the contrary of what occurred when land values rose rapidly from 1900 to 1920. Table III shows that for the west north central states as a whole, 51.8 per cent of the farms were mortgaged in 1920 as compared to 43.1 per cent in 1900. Another circumstance related to the foregoing is the probable reduced turnover of farms during this period. Only about a fifth as many sales of farm land were reported to the Minnesota Tax Commission during 1922-25 as during 1912-15, but the sales data from county records in two counties indicate that a large proportion of the sales in recent years have been recorded as for $1, hence are not reported to the tax commission.

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[5] During survey work in 1924 a farmer was interviewed in Pope county who sold 100 acres of land in 1917 to a German tenant for $12,000 upon a payment of $1,000 and the balance on contract for a deed. Many farms were sold during the land boom with very small payments down, and some have been sold in that way since.

Whenever sales fall off, the number of new mortgages written is likely to fall off also. Many of the transfers made, it has already been explained, were to the mortgage holders. It is also common belief based on observation that an unusual proportion of recent purchasers of farms could pay cash in full. The net effect of all the foregoing would be the elimination of many old mortgages and the writing of relatively fewer new ones.

TABLE II

CREDIT AND RELATED TENURE CHANGES IN MINNESOTA BETWEEN 1920 AND 1925

	1920	1925
1. No. of farms	178,478	188,231
Owner	132,744	136,382
Full-owner	112,880	112,906
Part-owner	19.864	23,476
Managed	1,596	766
Rented in full	44,138	51,083
2. Size in acres (all)	169.3	159.7
Full-owner	144.9	132.5
Part-owner	234.2	222.4
Managed	277.6	292.6
Rented	198.5	189.1
3. Value per acre (all)	$109.23	$ 79.63
Full-owner	$104.30	$ 80.85
Part-owner		$ 69.45
Managed	$113 37	$ 88.88
Rented	$120.85	$ 83.03
4. Full-owner and part-owner farms mortgaged		
No. mortgaged	69,545	66,319
Per cent of total reporting	52.4	48.6
No. farms unknown	9,113	*
5. Full-owner farms mortgaged		
No. reporting amount	57,585	52,184
Per cent of total reporting	51.1	46.2
Average value of farms	$16,080	$11,736
Average amount of mortgage	$4,419	$5,117
Ratio of mortgage to value	27.5	43.6
Average size, acres	†	144.6
Average value per acre	*	$ 81.13
6. Value of all mortgages‡	$445,731,000	$495,569,400

* Data not available.

† The 1920 census does not give size of mortgaged farms.

‡ This is an estimate. The census reports mortgage indebtedness for full-owner farms only. In this estimate the part-owner and the managed farms are assumed to have the same proportion of debt as the full-owner farms. The Bureau of the Census used this method in a 1920 estimate (mimeographed release). The mortgage debt in 1920 on rented farms was estimated as 11.7 per cent of the value of all rented farms. The Bureau of Agricultural Economics, U. S. Dept. Agr., obtained a figure of 9.2 per cent for the United States in a special survey made in 1920. It is here assumed that the debt on rented farms increased between 1920 and 1925 at the same rate as the encumbrance on full-owner farms, which increased from 14.3 to 22.1 per cent.

The principal circumstance making one doubt the adequacy of the above explanation is the actual increase of $700 in the average size of the mortgages during this period. So far as census data are available, there never has been a time when mortgages and land values have not increased together. During this period, however, many old mortgages were rewritten at higher amounts, in order to liquidate short-time debts incurred just before the break in prices of farm products, or to cover new losses arising from operations in 1921, 1922, and 1923. These increases may have been large enough to more than offset the decrease in size of mortgages written against new purchases after land values broke in 1921.

TABLE III

Percentage of Owned Farms Mortgaged in Minnesota Compared with Neighboring States and with the United States, 1890 to 1925

Area	1925	1920	1910	1900	1890
Minnesota	48.6	52.4	46.0	43.3	45.4
North Dakota	63.8	71.1	50.2	30.3	47.9
South Dakota	62.4	57.0	37.4	35.3	51.1
Montana	54.6	59.5	20.6	13.4	14.4
Iowa	55.6	54.2	51.2	52.1	52.8
Wisconsin	55.9	59.1	51.1	44.9	42.1
Illinois	35.5	38.5	38.4	37.9	36.3
East north central states*	39.4	42.6	40.5	38.5	37.1
West north central states†	51.2	51.8	45.6	43.1	47.3
United States	35.5	37.2	33.2	30.0	27.8

* Ohio, Indiana, Illinois, Michigan, and Wisconsin.

† Minnesota, Iowa, Missouri, North Dakota, South Dakota, Nebraska, and Kansas.

But this explanation takes no account of the fact that not only were old mortgages increased on many farms, but that some farms with no mortgages in 1919 now have mortgages. The effect of this is to increase the number of mortgages and decrease the average size, because such mortgages are likely to be small. If popular impression is in any way a safe guide in this matter, it suggests an increase in number of mortgages from this source that would more than offset the decrease from causes already mentioned.

If a considerable number with mortgages failed to answer the mortgage questions, as was suggested in the opening paragraph of the study, this would account for everything that appears in the data. It would give too small a percentage of mortgaged farms, but probably would not greatly affect the size of mortgages—there is little reason to suppose that more small mortgages would not be reported than large ones, or vice-versa.

Survey Data

Data on this point substantiate these conclusions. In the fall of 1924 a survey was made of 240 farmers in six areas in Minnesota located as indicated in Table IV. Of the 172 of these farmers who owned their farms, 106, or 65.5 per cent, had mortgages on them.

This is to be compared with the 50.4 per cent census average for the counties in which these areas are located. The 240 farmers were taken at random in each area. That they constituted fairly representative samples of the counties in which the surveys were made is shown by the close correspondence with the county averages in mortgage debt per farm and ratio of debt to value. Also, as shown in Table V, while there are slight differences in the average size of mortgaged farms when compared by counties, the average size of farms in six counties departs only 3 acres from the Census average for the six counties in which the survey was taken.

TABLE IV

COMPARISON OF DATA FOR 172 FARMS IN 6 COUNTIES WITH CENSUS DATA FOR 1925 AND 1920

Area	Survey				Census 1925			Census 1920		
	No. of owned farms	Per cent farms mortgaged	Ratio of debt to value	Mortgage debt per farm	Per cent farms mortgaged	Ratio of debt to value	Mortgage debt per farm	Per cent farms mortgaged	Ratio of debt to value	Mortgage debt per farm
Steele	30	60.0	40.2	$6,100	42.0	49.7	$7,620	49.8	30.6	$5,054
Cottonwood.....	13	84.6	40 0	9,763	60.5	44.4	9,880	66.8	24.8	5,334
Pope	30	50.0	40.0	5,700	50.5	37.9	5,194	52.3	26.7	3,592
Norman	20	85.0	49.7	4,812	53.9	40.8	4,519	53.4	26.6	2,620
Chisago	39	48.7	40.0	4,266	43.7	38.3	3,613	43.3	26.3	2,548
Hubbard	40	65 0	30.6	1,567	57.7	37.2	1,811	64.2	23.9	1,320
Average for all		65.5	40 3	4,776	50.4	42.4	5,072	53.4	26.7	4,257
Average for state		...	...	....	48.6	43.6	5,117	52.4	27.5	4,119

TABLE V

COMPARISON BY COUNTIES OF 1925 CENSUS AND 1924 SURVEY FOR SIZE OF MORTGAGED FARMS

	Steele	Cottonwood	Pope	Norman	Chisago	Hubbard	Average*
Census, 1925..............	135	190	190	157	100	132	146
Survey, 1924..............	107	197	176	234	112	115	149

* Average for state, 145 acres.

Moreover, the six surveys seem fairly to represent the state as a whole in both these respects. Of the 106 owner-operators who had mortgages on their farms in 1924, 36 did not have when the 1920 census was taken, 22 had been re-written at a higher amount, 32 had been renewed at the same figure, and only 16 had not been disturbed (Tables VI and VII). This represents a great deal of mortgage activity, making possible a considerable change in the mortgage status of the farmers. The point in which we are mainly interested here is the change in size of mortgages and percentage of farms mortgaged. Twenty-two mortgages were increased an average of $1,740, considerably more than the census average for the state; 36 new mortgages were written for an average of $4,680, somewhat less than the state average. The original data show that of the 36 new mortgages 8, averaging $2,071, were entirely to finance or cover indebtedness in connection with buildings or general farm expenses; 24, averaging $5,520, were to cover land purchases only; and 4, averaging $4,575, were to cover purchases plus building or other farm expenditures.

Unless the 28 new mortgages covering purchases represent a smaller proportion of farmers buying on mortgage than for the same number of farmers making purchases in these areas before 1920, the 8 new mortgages written for other purposes represent an addition to the percentage of farms mortgaged, and as their average is only $2,071, they would reduce the average size of all mortgages and offset in part the increase of $1,740 in the amount of the 22 old mortgages. As already indicated, more of the farmers buying recently may have paid cash in full, but surely not enough more to offset the 11 new mortgages. The sample is very small, however, and not too great reliance can be placed in it. It is entirely possible that more than 52.4 per cent of the farms in these areas were mortgaged in 1920; and that a careful survey then might have given a figure also over 60 per cent.

Calculations from the data in Table VI show that of the new mortgage debt for other than purchase, 62 per cent arose from new building operations, 8 per cent from purchase of new equipment, and 30 per cent from general farm expenses, chief of which was taxes. In Hubbard County three of the farms borrowed on mortgages to clear land. The new mortgages written for these purposes in 1920, 1921, and 1922 were mostly to cover obligations incurred before the break in farm prices came, and were carried for a time on notes or open accounts. The new mortgage debt incurred for these purposes in 1923 and 1924 represented the beginnings of a revival of agricultural development.

Additional evidence of the same general nature is contained in the results of two surveys of rural living in Minnesota made in 1925 and 1926, respectively.[6] The 1925 survey included 123 owner operators who paid at least $125 interest on mortgage and other debts (about $25 in one new cut-over county). At least 60 per cent had mortgages on their farms, as compared with the 1925 census average of 47 per cent. The 1926 survey included 149 owners who paid at least $125 interest on mortgage and other debt (about $100 in one partly cut-over county). At least 64 per cent had mortgages on their farms as compared with 52 per cent in the 1925 census. The two surveys include 12 sections well distributed over the state, and the farmers were chosen entirely at random.

[6] Unpublished data from surveys made by Carle C. Zimmerman, Rural Sociologist, Minn. Agr. Expt. Station.

TABLE VI

MORTGAGES OF 172 OWNER FARMERS IN MINNESOTA WRITTEN OR INCREASED BETWEEN 1920 AND 1924

(Classified according to purposes.)

County	No. of farms	Old mortgages renewed*		Old mortgages increased							
				To buy more land		To finance new buildings		To purchase equipment		To finance general expenses	
		No.	Amount	No.	Amount	No.	Amount	No.	Amount	No.	Amount
Steele	16	10	$ 42,700	0	$ 0	2	$ 3,500	2	$1,000	0	$ 0
Cottonwood	8	5	56,800	0	0	0	0	0	0	0	0
Pope	14	11	53,960	0	0	3	8,140	1	1,000	2	5,000
Norman	16	9	41,600	2	5,000	2	2,600	3	2,500	4	3,000
Chisago	14	6	18,700	0	0	0	0	0	0	0	0
Hubbard	21	13	19,300	0	0	2	2,500	1	800	4	3,200
All areas........	89†	54	$233,060	2	$5,000	9	$16,740	7	$5,300	10	$11,200

* Twenty-two renewed for higher amount, 32 at same amount.

† Not including 16 mortgages not disturbed.

County	Old mortgages increased all purposes*		New mortgages									
			To buy land		To erect buildings		To buy equipment		To finance general expenses		All purposes*	
	No.	Amount	No.	Amount	No.	Amount	No.	Amount	No.	Amount	No.	Amount
Steele	2	$ 4,500	4	$34,600	3	$14,700	0	$ 0	1	$1,000	6	$ 44,900
Cottonwood	0	0	3	23,600	0	0	0	0	0	0	3	23,600
Pope	6	14,140	1	7,000	2	2,500	0	0	1	900	3	10,400
Norman............	7	13,100	8	27,800	0	0	0	0	2	3,800	8	31,600
Chisago	0	0	7	35,000	2	7,700	0	0	1	1,000	8	43,700
Hubbard	7	6,500	5	4,500	1	1,500	0	0	2	2,750	8	8,750
All areas......	22	$38,240	28	$132,500	8	$26,400	0	$ 0	7	$9.450	36	$168.350

* The number of mortgages does not total as given because some mortgages were written for more than one purpose.

TABLE VII

MORTGAGES OF 172 OWNER FARMERS IN MINNESFTA WRITTEN OR INCREASED BY YEARS BETWEEN 1920 AND 1924

(Classified according to purposes.)

Years	No. of farms	Old mortgages renewed		Old mortgages increased							
				To buy more land		To finance new buildings		To purchase equipment		To finance general expenses	
		No.	Amount	No.	Amount	No.	Amount	No.	Amount	No.	Amount
1920	10	3	$ 13,500	0	$ 0	0	$ 0	0	$ 0	1	$ 4,500
1921	17	4	9,100	0	0	1	600	1	500	2	700
1922	18	13	70,800	1	2,000	2	4,000	0	0	2	1,100
1923	16	10	35,200	0	0	2	3,500	2	1,500	1	400
1924	28	24	104,460	1	3,000	4	8,640	4	3,300	4	4,500
All years	89	54	$233,060	2	$5,000	9	$16,740	7	$5,300	10	$11,200

Years	Old mortgages increased all purposes*		New mortgages									
			To buy land		To erect buildings		To buy equipment		To finance general expenses		All purposes*	
	No.	Amount	No.	Amount	No.	Amount	No.	Amount	No.	Amount	No.	Amount
1920	1	$ 4,500	8	$ 27,900	2	$ 6,500	0	$ 0	1	$1,000	7	$ 35,400
1921	2	1,800	10	58,800	5	18,900	0	0	1	1,000	13	78,700
1922	5	7,100	5	11,700	0	0	0	0	2	4,800	5	16,500
1923	3	5,400	3	9,200	1	1,000	0	0	2	1,150	6	11,350
1024	11	19,440	5	24,900	0	0	0	0	1	1,500	5	26,400
All years	22	$38,240	28	$132,500	8	$26,400	0	$ 0	7	$9,450	36	$168,350

* The number of mortgages does not total as given because some mortgages were written for two or more purposes.

In the 1926 survey, 59 owner farmers in two areas were studied especially from this point of view. On January 1, 1925, when the census was taken, 35, or 60 per cent of the 59, had mortgages on their farms. The nearest comparable 1925 census figure is 48 per cent. Fourteen of these 35 mortgages had been written since January 1, 1920. Eight were new mortgages; and 6 were old mortgages renewed, all for an increased amount. Of the 8 new mortgages, 3 were entirely to purchase land and one was for the purpose of buying more land and covering general expenses. The rest were for buying equipment, erecting buildings, and covering general expenses. The average size of the 6 old mortgages was $18,000 before renewal and $23,400 after renewal. The new mortgages averaged only $6,100. The nearest comparable average mortgage debt, as shown by the 1925 census, for these two areas was $9,000. The survey data show about $9,600. The old mortgages renewed are larger than the census average shown and the new mortgages are less.

Between January 1, 1920, and January 1, 1925, only 13 of the 35 mortgaged owner-operators covered in the survey made any payments on the principal. One of these resulted from a sale of part of the land and another from inheritance. The average for the remaining 11 was $1,260, or $252 per year. This is an extremely poor showing and indicates forcefully the severity of the present agricultural depression. From January 1, 1925, to the time the survey was made only 8 had made payments on the principal of their mortgages.

Further evidence that the census data are too low is found in a survey made at the beginning of 1924 in Kittson, Marshall, Polk, Red Lake, and Wilkin Counties by the Division of Agronomy and Farm Management, of the University of Minnesota, under the supervision of Dr. Andrew Boss. Of 106 owner farms studied, 90, or 83 per cent, were mortgaged. The 1925 census average for these counties is 61 per cent. Even allowing for the fact that the sample probably was not entirely random, as indicated by a considerably larger average value and size of farms than was reported by the 1925 census, there is still evidence that the census data are too low.

It seems that there is more mortgage indebtedness on Minnesota farms than the 1925 census data indicate. The 1920 census data, also, may be too low. We can not be sure, therefore, that the number of farms mortgaged has increased since 1920.

The impression is common among farm mortgage agencies in the Northwest that there has been a considerable increase in mortgage indebtedness. From the end of 1919 to 1924, federal land bank loans in Minnesota made a net increase of 135 per cent and the number of loans increased from 4,052 to 7,729, or 91 per cent. The volume of joint stock land bank loans increased 46.6 per cent. Net loans of insurance companies increased 104 per cent between 1919 and the end of 1923. The Minnesota Rural Credit Bureau began to operate in 1923 and by the end of 1924 had loaned approximately 32 million dollars, involving a little more than 6,000 loans. The loans made since 1920 by the Minnesota Rural Credit Bureau, the Federal Land Bank of St. Paul, the joint stock land banks, and insurance companies are recorded in Table XXV. The farm mortgage companies report an increase in volume of business with the exception of some private investment companies.

Table II estimates, even on the basis of the census figures, an increase of $49,000,000, or 11 per cent, in the total farm mortgage indebtedness. The rest of the apparent increase mentioned may merely represent a shifting to those agencies of mortgages formerly held by banks, private institutions, and individuals. This no doubt occurred in large volume, especially from banks to the Minnesota Rural Credit Bureau, but it hardly seems that such shifting could account for all the increase in volume of loans reported by the loaning institutions named.

Changes Since 1890

The 1890 census was the first to report the percentage of farms mortgaged. Table III traces the changes that have taken place in Minnesota and neighboring states and for the United States as a whole. In several of the west north central states, especially the Dakotas and Minnesota, there was a decline between 1890 and 1900. The group as a whole showed a decline from 47.3 per cent in 1890 to 43.1 per cent in 1900. This no doubt reflects the rapid expansion to new lands and the homestead movement that was going on during this period. For the rest of the states in the Northwest and even the states mentioned, since 1900, and for the United States as a whole, as indicated in Figure 1, the percentage of farms mortgaged has gradually increased. For the United States as a whole it has been at the rate of about 3.0 per cent each ten years. As there was a decline of 1.7 per cent from 1920 to 1925, there will be less than the usual increase in the present decade, unless a rapid swing forward sets in soon, or unless the census data are in error, as above suggested.

There is nothing alarming about this increase. In fact, it would be remarkable if it had not occurred. The average value of farms in Minnesota and the west north central group of states multiplied by six between 1890 and 1920, and multiplied by more than two when prices are expressed in terms of dollars of the same value, that of the year 1925 (Table VIII). The decline in values between 1920 and 1925 was only a little more than the decline in the general price level. If no more farms were mortgaged now than in 1890, the situation would be that those buying farms now, many of them young men buying their first farms, at an average of $12,717, are as able to pay cash for them, or are able to pay off their mortgages as rapidly as when farms were worth $2,910 on the average. These $2,910 in 1890 were worth $5,728 in dollars of 1925. Surely it can not be said in fairness that Minnesota farmers are going backward just because they have not quite kept up in wealth with the rapid increase in land values. As before stated, it would be remarkable if they had kept up.

TABLE VIII

Increase in Value of Farms from 1890 to 1925

Year	Values in actual dollars			Values in 1925 dollars			Index number used*
	United States	West north central states	Minnesota	United States	West north central states	Minnesota	
1925	$ 7,776	$14,875	$12,717	$8,125	$15,543	$13,288	95.7
1920	10,284	22,307	18,496	7,584	16,450	13,640	135.6
1910	5,471	10,464	8,085	8,456	16,173	12,496	64.7
1900	2,896	4,385	4,329	5,701	8,632	8,522	50.8
1890	2,909	3,245	2,910	5,726	6,388	5,728	50.8

* Bureau of Labor index of wholesale prices, expressed in terms of prices in 1925. For 1910, 1920, and 1925, the index used is the average of the monthly indexes for the six months preceding the date of taking the census.

In this connection, it must not be forgotten that a good part of the value of our farms must be earned on the land in each generation. One farmer pays off his mortgage, sells his farm, and moves to town with all his wealth. The man who buys it probably has to start with a new mortgage. Or perhaps the farmer passes the farm on to one of his sons, in which case the son who gets the farm probably has to mortgage it to pay the other heirs. Only if land values were standing still and if farms were being passed to heirs unencumbered, could it be said that agriculture was not holding its own if the percentage of mortgaged farms was increasing. Agriculture in the United States is doing far better than that—it is keeping nearly constant the percentage of farms mortgaged, at the same time financing the transfer to the cities of a large group of retired farmers in each generation and paying off a large group of heirs who have left the farm. It has financed a large part of the expansion of agriculture that has taken place when some of the other sons have been helped to start in new farming areas. It has also provided the education (often not very good) for the young people who leave the farms for the city. The flow of wealth from the city to the country is a mere dribble compared with all this in the other direction.

The Farm Owner's Equity

It is the custom of many persons to focus attention upon the absolute size of the farm mortgage today as compared with that in earlier times, and to point out, as is done in Table IX, that the mortgages averaged $5,117 in 1925 and only $814 in 1890, and thus make it appear that the farmers are getting more and more in debt on even the farms that they own.

TABLE IX

Changes in Mortgage Debt and Owners' Equities on Mortgaged Owner-Operated Farms, Minnesota, 1890 to 1925

Year	Value per farm	Mortgage debt per farm	Owner's equity per farm	Percentage increase in debt	Percentage increase in equity	Ratio of debt to value
1925............	$11,736	$5,117	$ 6,619	15.8	—43.2	43.6
1920............	16,080	4,419	11,661	137.1	124.3	27.5
1910............	7,062	1,864	5,198	62.4[*]	85.0[†]	26.4
1900............	3,957[‡]	1,148[§]	2,809	41.1	59.6	29.0[*]
1890............	2,574	814	1,760	...	...	31.6

[*] Increase 1890 to 1910, 129 per cent.

[†] Increase 1890 to 1910, 195.3 per cent.

[‡] Estimated. The average value of mortgaged farms in 1920 and 1910 is nearly the same as the average value of all fully owned and partly owned farms. For 1920, the respective figures are $16,511 and $16,080; and for 1910, $7,538 and $7,062. For the two periods, the average value of owned farms exceeds that of mortgaged farms by 4.5 per cent. It is assumed that about the same relation existed in 1900. The average value of owned farms in 1900 was $4,070, which, reduced by 4.5 per cent, amounts to $3,957.

[§] The ratio of debt to value in 1890 and 1910 for mortgaged farms is given in the census. The ratio in 1900 is estimated at 29 per cent by interpolation from 1890 and 1910.

Table IX sets over against these figures the increase in the owner's equity per farm, that is, the value of the farm over and above the mortgage. It appears that from 1890 to 1910 the equities increased more rapidly than the debt, and from 1910 to 1920 only a little less rapidly. While the total mortgage debt of all the owner farms of Minnesota was increasing from $37,709,000 in 1890 to $254,475,000 in 1920, or 575 per cent, the owner's equities were increasing from $176,552,000 to $1,877,000,000, or 963 per cent. Relatively, the farmers were getting less in debt. At least, they were getting more out of debt. This relationship is usually stated in terms of the ratio of debt to value of mortgaged farms, as in the last column of Table IX. The mortgaged owner-operators of Minnesota farms owned all but 27.5 per cent of the value of their farms in 1920, as compared with all but 31.6 per cent in 1890.

All these figures are expressed in terms of the dollar of 1925 in Table X. It thus appears that even absolutely the debt increased very little from 1890 to 1920. The increase from $814 to $4,419 in mortgages on Minnesota owner-operated farms now appears to have been an increase only from $1,602 to $3,259, or 103 per cent.

TABLE X

CHANGES IN MORTGAGE DEBT AND OWNERS' EQUITIES ON MORTGAGED OWNER-OPERATED FARMS, MINNESOTA, 1890 TO 1925, EXPRESSED IN DOLLARS OF 1925

Year	Wholesale price index*	Value per farm, 1925 dollars	Mortgage debt per farm, 1925 dollars	Owner's equity per farm, 1925 dollars	Percentage increase in debt	Percentage increase in equity
1925	95.7	$12,263	$5,347	$6,916	64.1	−19.5
1920	135.6	11,855	3,259	8,596	13.1	7.0
1910	64.7	10,915	2,881	8,034	27.5	45.3
1900	50.8	7,789	2,260	5,529	41.1	59.6
1890	50.8	5,066	1,602	3,464	...	...

* Bureau of Labor Statistics, index of wholesale prices reduced to 1925 basis. For 1910, 1920, and 1925, the index used is the average of monthly indexes for the six months preceding the date of taking the census.

To explain the abrupt change after 1920, other circumstances should be considered. A large proportion of the mortgages in force in 1925 were contracted between 1918 and 1921, when land prices were high. Most of those that were drawn for five years have been renewed. The value of the average mortgaged owner-operated farm in Minnesota has declined from $16,080 in 1920 to $11,736 in 1925. If there had been no increase in the average size of the mortgages, if it had remained at $4,419 instead of increasing to $5,117, the ratio of debt to value would still have increased from 27.5 per cent to 37.5 per cent, owing to the decline in land values, and the owners' real equities would have fallen off 37.2 per cent during the five years.

How this increase has worked may be illustrated by a particular farm, bought, let us say, in 1919, for $21,000.

	1919		1925
Bought for	$21,000	Could be sold for	$16,000
Paid cash	14,000	Payments on principal	none
Mortgage	7,000	Mortgage	7,000
Equity	14,000	Equity	9,000
Equity in 1925 dollars	10,728	Equity in 1925 dollars	9,000
Ratio debt to value	33.3	Ratio debt to value	43.7

If the operator had paid off $1,000 on the principal in 1920 and just held his own since, his ratio of debt to value would be 37.5 instead of 43.7 in 1925. If this operator, while paying nothing on his principal, had increased his mortgage to $8,000 when renewing it, his ratio of debt to value would be 50.0 instead of 43.7 in 1925. The opposite of this was taking place between 1890 and 1920, when land values were rising. A farmer who paid $5,000 cash on a $10,000 farm in Minnesota in 1910, without paying a cent on the principal, had his equity increased from $5,000 to approximately $19,000 by January, 1920, land values increasing from $45 to $109 per acre, or 142 per cent, during that period. Even when this $5,000 and $19,000 are expressed in the 1925 price level, the real equity on the farm had increased from $7,728 to $14,112. From 1890 to some time after 1910, the effect of this in raising owners' equities in mortgaged farms was so great that it more than offset the increasing number and size of mortgages.

Since 1920-21 transfers of land have been fewer and old mortgages have been largely renewed at their original high figures, with the result that the mortgaged owners' real equity in the farm is less today than it was in 1910. This is a serious situation. It means that a large part of the material gains from agricultural progress since 1910 have been wiped out so far as the present generation of farmers is concerned.

Movements in Land Prices

Nor is it proper to lay the blame for much of this on the agricultural population. Figure 2 shows that movements in the general level of prices have been the major factor in the movement of land values. A permanent change in general price levels should be fully and immediately reflected in land prices. Most of the small movements in price level, however, are obviously temporary, and farmers, like other business men, can be expected to adjust their business affairs on this assumption. By no means do all business men so adjust their affairs; but we still insist that they should, and we ask the same of farmers. The longer contin-

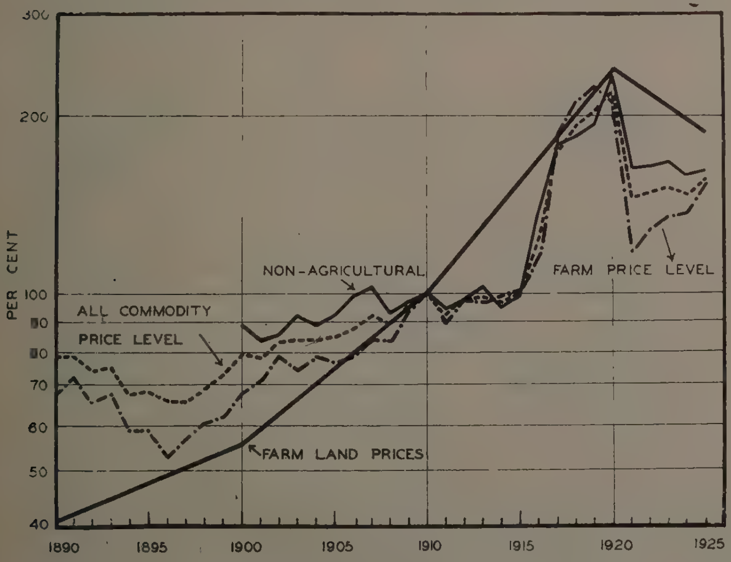
RELATION OF LAND PRICES TO OTHER PRICE LEVELS,
BASIS 1910 CONDITIONS

Fig. 2. Changes in prices of Minnesota farm land from 1890 to 1925, compared with changes in all commodity and other price levels. In general, the movements of land prices have followed movements in the general level of prices.

uous movements of the price level, however, such as from 1897 to 1916, nearly everyone takes at face value, and until more is known about them and their causes, there is nothing else to do. The rapid upward price level movement from 1917 to 1920, followed by the sudden downward movement of 1921 and 1922, belongs in the class of short-time swings which should have been recognized as such and discounted. But business in general failed to do this, and it would be unfair to hold the agricultural class especially at fault for their failure in this respect. A sharp break in prices was expected immediately at the close of the World War. When it did not come, but was followed by a second period of inflated prices, both business men and farmers lost their balance. Some eminent economists concluded that the new high price level had come to stay. That they were partly right is evidenced by the fact that price levels have not yet returned to their pre-war level, but for several years have been fairly stable at between 50 and 60 points above the pre-war level, and that there are better reasons for

RELATION OF LAND PRICES TO COMMODITY PRICE LEVELS, BASIS 1890 CONDITIONS

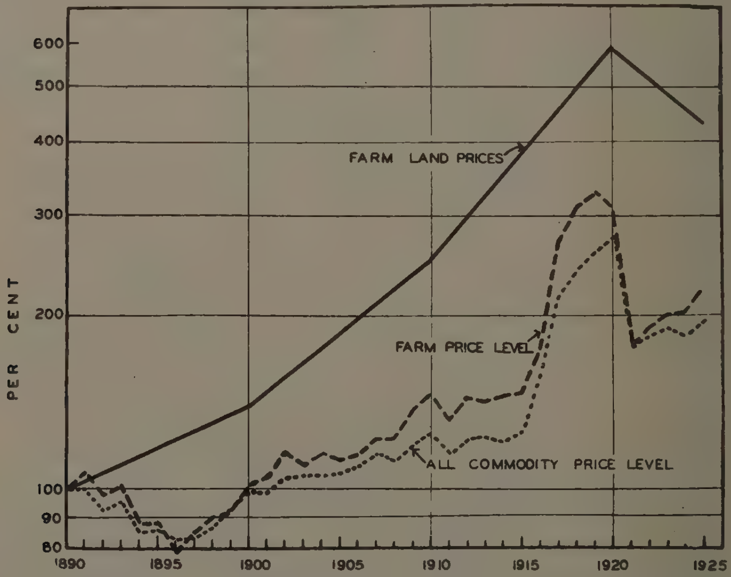

Fig. 3. This chart is like Figure 2 except that it starts with 1890 as the base point of 100 (data in Table XI). This means that the curves compare conditions at any point with those in 1890. It appears that prices of farm products have been above the all-commodity or general price level ever since 1900 except for a brief period in 1921, and that they are now considerably higher relatively. Farm land prices rose until 1920. They rose from 1890 to 1900 when prices were just holding their own. There was a large increase in improved land during this decade (Table XII).

believing they will not decline far than for thinking they will sink to the level of 1913.

Farm land prices in Minnesota rose considerably faster than the general price level, from 1910 to 1920, and have declined at about the same rate since (Fig. 2 and Table XI). The net result of the whole movement is a farm land price now 75 per cent above 1910, and a general price level only 57 per cent above 1910. Data of the Minnesota Tax Commission show that from 1914-15 to 1920 land values rose only 96 per cent as compared with 130 per cent for the general price level.

This does not mean, however, that farm land prices are now too high. Included in the value of farm land is the value of buildings. It appears that even when adjustment is made for the changing price level, buildings increased in value per acre during the period (Table XII). Improvement in roads and transportation should also help to make land values rise faster than the general price level.

TABLE XI

COMPARISON OF MOVEMENT OF MINNESOTA FARM VALUES AND COMMODITY PRICE LEVELS, 1899 TO 1925

	Value of farm land per acre	Index numbers 1910 = 100				Index numbers 1890 = 100		
		Value of farm land per acre	Farm commodities	All commodities	Non-agricultural products*	Value of farm land per acre	Farm commodities	All commodities
1890........	$ 18.22	39.9	79.6	67.6	...	100	100	100
1900........	25.21	55.3	79.6	68.2	89	140	101	100
1910........	45.62	100.0	100.0	100.0	100	250	148	126
1920........	109.23	239.4	223.3	211.1	236	599	312	280
1925........	79.63	174.6	157.3	153.1	161	437	226	197

* Index on 1910-14 basis back to 1910 obtained from supplement to Agricultural Situation, p. 30. Index from 1900 to 1910 obtained by letter from Bureau of Agricultural Economics, Washington, D. C.

The percentage of land improved has remained nearly constant since 1900. This is because new land has been taken into farms at about the same rate that land already in farms has been cleared.

TABLE XII

CHANGE IN IMPROVEMENTS PER ACRE ON MINNESOTA FARMS, 1890 TO 1925

	Percentage of farm land improved	Census value of buildings per acre	Value of buildings per acre in dollars of	
			1910*	1925*
1890..................	59.6	†	....	....
1900..................	70.3	$ 4.20	$ 6.43	$10.63
1910..................	71.0	8.79	8.70	14.53
1920..................	71.1	18.23	11.70	19.35
1925..................	‡	19.86	12.01	19.86

* Adjusted on the basis of an index compiled from value of building material and wages of labor, with allowance for the fact that the census valuations always lag behind current prices.

† Not available.

‡ Not obtained in 1925 census—probably a slight increase.

More important than either of the foregoing is the fact that prices of farm products rose much faster than other prices from 1900 to 1915. The index for prices of farm products rose 32 points during the period; for non-agricultural products, 10 points; and for the general price level, 21 points. This is shown clearly in Figure 2.

Subtracting the adjusted value of buildings given in Table XII from the value of land and buildings at each decade, both expressed in 1925 dollars, gives the values in the last column of Table XIII. The increase since 1890 is no more than is warranted by the land improvements and the rise of prices of farm products above that of the general price level.

TABLE XIII

VALUE PER ACRE OF LAND AND BUILDINGS, BUILDINGS, AND LAND ALONE, MINNESOTA, 1890 TO 1925

	Value of land and buildings, 1925 dollars*	Value of buildings, 1925 dollars†	Value of land, 1925 dollars
1890	$35.86	‡	‡
1900	50.21	$10.63	$39.58
1910	70.52	14.53	55.99
1920	80.55	19.35	61.25
1925	83.21	19.86	63.35

* It is assumed that the estimate for land and buildings combined is not affected by the lag in valuation of buildings.

† From Table XII.

‡ Data not available.

Changes in Size and Number of Farms

Somewhat related to changes in mortgage debt are changes in size and number of farms. The land in farms in Minnesota increased until 1920 (Table XIV). The figures for the 1900 census are usually considered much too high because of the method of taking that census. This has accentuated the increase for that decade, and reduced the increase for the following decade. The rate of increase between 1910 and 1920 was only 9.2 per cent. The slight decrease since 1920 may actually represent a certain amount of abandonment of land that took place in certain parts of the state; but more likely it represents omissions in census taking. The large increase in number of farms between 1920 and 1925 is also believed by many to be due in considerable part to the method of taking the 1925 census. While the total acres for farms have been decreasing, the number of improved acres increased until 1910. The 1925 census obtained no data as to improved land, but an estimate on the basis of crop acreage would be about 115 acres.

Small farms are to some extent a substitute for mortgage debt. The smaller the farms purchased, the more likely they are to be paid for in full, or nearly so. On the other hand, if farms are too small, those who purchase them on mortgages will pay off the mortgages slowly. The more valuable the mortgaged farms in Minnesota are, the greater is the tendency for a higher percentage of their value to be mortgaged (Fig. 4). This relationship does not always hold true because of other conditions which may conceal the general tendency.

TABLE XIV

NUMBER OF FARMS, ACRES OF LAND IN FARMS, ACRES PER FARM, AND IMPROVED ACRES PER FARM IN MINNESOTA BY CENSUS YEARS, 1890 TO 1925

Census year	Number of farms	Acres of land in farms	Acres per farm	Improved acres per farm*
1925	188,231	30,059,137	159.7	125.0†
1920‡	178,478	30,221,758	169.3	120.4
1910	156,137	27,675,823	177.3	125.8
1900	154,659	26,248,498	169.7	119.2
1890	116,851	18,663,645	159.7	95.2

* "Improved land includes all land regularly tilled or mowed, land in pasture which has been cleared or tilled, land lying fallow, land in gardens, orchards, vineyards, and nurseries, and land occupied by farm buildings." Census 1920, Vol. V, p. 23.

† Not reported in 1925 census. Figures are estimated by finding ratio between improved land and crop land harvested as reported for 1919 in the census of 1920 and assuming the same relationship between crop land harvested and improved land in 1924. If data for land in farmsteads were available in the 1925 census a more direct method of computing would be available.

‡ Data 1890 to 1925. See 14th census, Vol. V, p. 47.

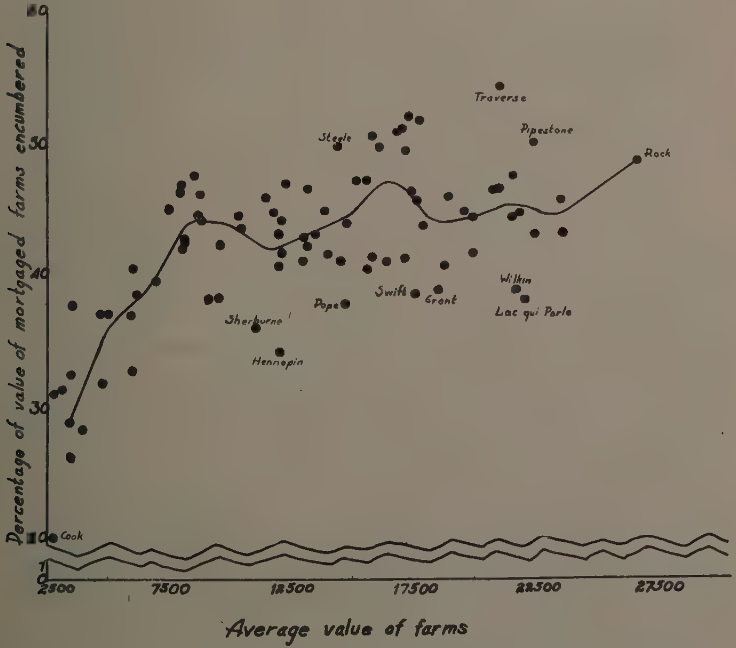

Fig. 4. Increase in Mortgage Indebtedness with Value of Farms, by Counties, 1925

Change in Tenancy

It is not always realized that tenant farming and mortgage indebtedness are substitutes one for the other. The sooner young men are able to buy farms on mortgages, the less tenancy there will be. The percentage of Minnesota farms rented has increased from 12.9 to 27.1 since 1890 (See Appendix, Table III), about 3 per cent each ten years. In the five years from 1920 to 1925 the increase was 2.4 per cent as compared with 3.7 per cent during the preceding ten years. This represents an appreciable speeding-up of the rate of increase since 1920. In absolute numbers, there were 6,945 more tenants in 1925 than in 1920, and only 26 more full owners. This increase in number of rented farms is due to the fact that many tenants have remained tenants who in ordinary times would have bought farms under mortgages. They have done this (1) because they have saved little during the last five years, (2) because they have been waiting for the price of land to reach bottom before buying, (3) because the old incentive to purchase in order to realize upon the rise in value of land has been weakened considerably, and in some cases (4) because they have been marking time while waiting to decide whether or not they should continue farming. Some part of the increase in tenancy is no doubt due to foreclosures. Most of those who have had farms come back into their hands have rented them to farmers' sons wanting to become tenants, to farmers who have lost their farms, or to neighboring farmers who have operated them as additional rented land. That the last has happened frequently is demonstrated by the increase of 3,612 (18 per cent) in the number of partly owned farms during this period.

The "Agricultural Ladder"

The relation between tenancy and mortgage indebtedness is so immediate that it is worth while to analyze tenancy in some detail. It has been customary to assume that tenancy is merely a step, or rung, in the ladder by which the farm population ascends to full ownership; that most tenants were formerly laborers and eventually became mortgaged owners and then owners free of mortgage. To this succession of tenure stages, the term "agricultural ladder" has commonly been applied. In 1920, out of each 1,000 male persons 10 years of age or over working on Minnesota farms, 166 were laborers on the home farms, 200 were laborers on other than home farms, 156 were tenants, 6 were managers, 246 were mortgage owners, 193 were owners free of mortgage, and the status of 33 was unknown. This gives a clear picture of the relative importance of the steps in the agricultural ladder in Minnesota. Roughly, 37 per cent were in the labor stage, 16 per cent were in the tenant or manager stage, and 47 per cent were in the owner stage, of whom more than half had mortgage debt.

Not all farmers, however, pass over the same route to ownership. The "agricultural ladder" is too simple a description of what happens. Some pass directly from farm laborers on the home farms to tenants, and some work as laborers on other farms before becoming tenants. In the former case, probably the parents help the son or son-in-law financially. Many get enough help from parents that they omit the tenant stage altogether. Some inherit the home farm in full or in part, in the latter case having to pay off the other heirs. Some earn money while working in cities, mines, or forests that is used as cash payments on land purchases. The last is especially true in the cut-over section of the state.

TABLE XV

HOW FARM OWNERS ACQUIRED STATUS IN FOUR SOUTHERN MINNESOTA COUNTIES*

	Per cent
Home farm to owner (never were tenants)	40.0
Home farm to hired laborer to owner	21.6
Home farm to hired laborer to tenant to owner	14.5
Home farm to tenant to owner	13.4
Other industry to owner	5.7
Other industry to hired laborer to owner	1.5
Other industry to hired laborer to tenant to owner	2.2
Other industry to tenant to owner	1.1

* Courtesy of Dr. W. J. Spillmann. These unpublished data were obtained in a survey of 738 owner farmers in four southern Minnesota counties by the United States Department of Agriculture in 1917.

Many owners do not climb to ownership over all the rungs of the agricultural ladder. Only 14.5 per cent of those raised on the farm and 2.2 per cent of those coming from other industries among 738 owner farmers in 1917, were first farm laborers working out, then tenants, and finally owners (Table XV). About one-tenth of the owners came from other industries. This figure is too high for the period since 1921. The recent depression in agriculture has reduced the rate at which people go from other industries into agriculture. Of the 90 per cent who came out of agriculture direct, 21.6 per cent omit the tenant stage only, 13.4 per cent the hired laborer stage only, and 40.0 per cent both. A total of 36.1 per cent included the hired laborer stage somewhere, and 27.9 per cent the tenant stage. To these figures may be added 3.7 per cent for hired laborers and 3.3 per cent for tenants that came out of other industries.

Inquiries as to farm experience were included in the 1920 census for the first time. Of every 100 Minnesota farm owners in 1920, 38 reported previously operating a farm as a tenant and 45 reported working on a farm for wages. For each 100 in the tenant stage in 1920, 57 had previously worked for wages. These percentages are little higher than those in Table XV, which include only four southern counties in 1917.

Figure 5 is conclusive evidence that there is such a thing as an agricultural ladder. As farmers grow older, a smaller and smaller percentage are tenants. In 1920 less than 14 per cent of those from 45 to 54 years of age were tenants, as compared with 65 per cent of those under 25 years. Figure 5 also shows that between 1890 and 1920 the percentage of tenants in each group increased very perceptibly. In the most numerous group, 25 to 34 years old, for example, only 21 per

PERCENTAGE OF TENANCY IN EACH AGE GROUP FOR FARM CENSUS YEARS FROM 1890 TO 1920 FOR MINNESOTA

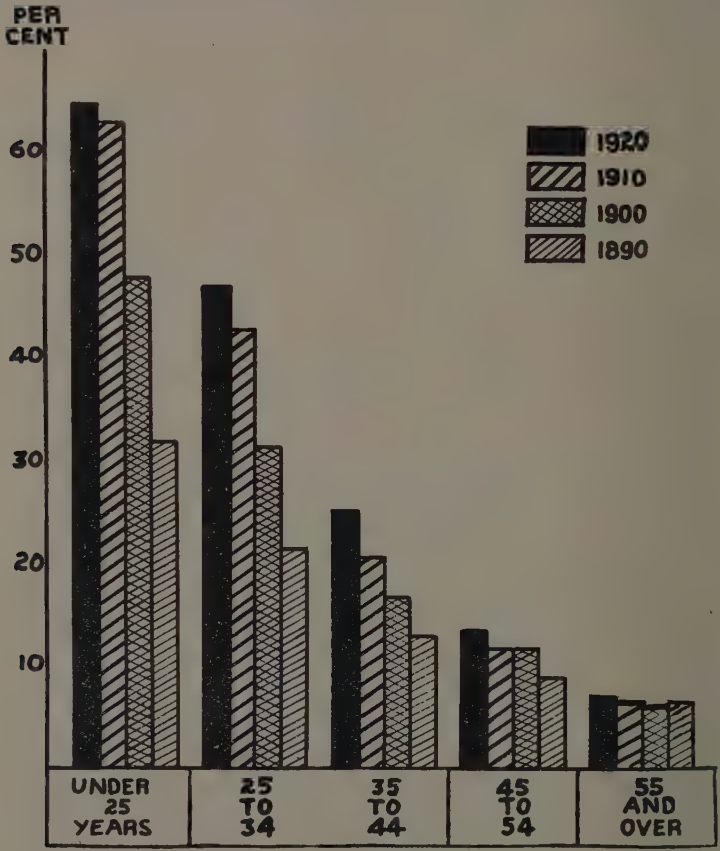

Fig. 5. As farmers grow older a smaller and smaller percentage of them are tenants. Between 1890 and 1920 the percentage of tenants in each age group increased very perceptibly. This chart indicates that the rate of ascent on the agricultural ladder is declining. Data from Tenancy in United States, Census Monograph IV, p. 92.

cent of the farm operators were tenants in 1890, as compared with 47 per cent in 1920.

There is further evidence in Figure 5 that the rate of ascent of the agricultural ladder is slowing down. Between 1890 and 1910 the percentage of tenancy increased most rapidly in the lowest age group; in the next decade, in the 25-to-34 age group; and between 1910 and 1920, in the 35-to-44 age group. Between 1910 and 1920 the change is very pronounced. This could indicate, however, that fewer young men are now passing through the tenancy stage, and those that became tenants while young are still tenants in unusual numbers. Up to 1900, at least, it seems that farmers' sons were becoming tenants at earlier ages. The smallness of the increase in the 25-and-under group between 1910 and 1920, is probably accounted for by the fact that the war experience kept more than the usual number of farmers' sons from becoming tenants. There is little evidence of an increasing "permanent tenant" class. In 1890, but 66 out of every 1,000 farm operators in Minnesota were still tenants at 55 years of age and over; and in 1920, the number had increased to only 70.

INCREASE IN LABORERS AND TENANTS, 1880 TO 1910

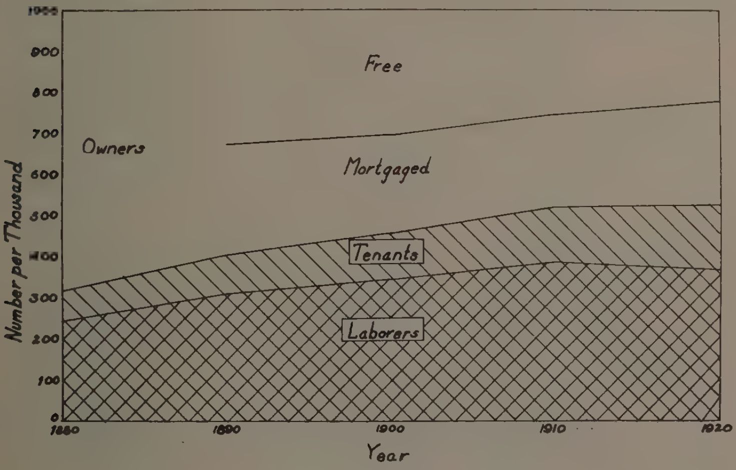

Fig. 6. Laborers as well as tenants increased faster than owners in Minnesota from 1880 to 1910. Between 1910 and 1920 both owners and tenants increased in relative numbers. This may reflect the decrease in size of farm families and the growing tendency of farm boys to leave the farms early in life.

The whole story of the agricultural ladder can not be told, however, in terms of tenants and owners. Tenancy takes the place of the farm laborer stage as well as of the owner-operator stage. Laborers working on Minnesota farms were increasing more rapidly than tenants in actual numbers from 1880 to 1910. There were 141 more farm laborers in each 1,000 in 1910 than in 1880, as compared with an increase of only 60 in the number of tenants in the same period. Both tenants and laborers were increasing at the expense of owner operators and as has already been pointed out, free owners at the expense of mortgaged owners. Between 1910 and 1920, however, both owners and tenants increased in relative numbers. The decrease in laborers was in those working at home. This probably reflects the decrease in size of farm families and the growing tendency of farm boys to leave the farms early (Fig. 6).

The census of 1925 reports 35 per cent of all cash tenants and 30 per cent of all share or other tenants in Minnesota as renting from relatives. A study of cash rents made by the United States Department of Agriculture in 1920 showed that cash rents on farms rented from relatives averaged nearly a third less than on other farms in Iowa and southern Minnesota.[7] In the rest of Minnesota the difference seemed to be less, but still was significant. Share leases also favor tenants that are related to the landlords.

Tenancy in Relation to the Credit Problem

It is not the purpose of this study to analyze the tenancy problem, but merely to show its relation to the credit problem. Young men ordinarily become tenants because they do not have money enough or financial backing enough to buy farms. If they could get more financial backing, or credit on less security, fewer would be tenants and more would be owners. Also, many would become tenants sooner than at present. But these would not necessarily be desirable changes. It is a mistake to have young men become tenant operators before they are old enough and experienced enough to become successful managers. It is an even more serious mistake for them to become owner operators before they are ready. As long as they have only limited capital, they can earn a larger return upon it by using it as a tenant's working capital than as an owner's fixed investment in land. Working as a farm laborer, even as a hired laborer away from home, is an excellent experience for a young man. This is especially true if his employer is more successful or more progressive than his father, which is often the case. Tenancy, especially on a share basis, is a valuable apprenticeship in farm management, especially if under a progressive landlord or one who has been a successful manager. More liberal credit arrangements, therefore, might easily do more harm than good. They would lead to a waste of the human and soil resources of the nation.

[7] Relation of Land Income to Land Values, by C. R. Chambers, U.S. Dept. Agr. Bull. 1224, pp. 54, 100-102. 1924.

On the other hand, keeping a young man a farm laborer after it is time for him to marry and establish a home for himself is extremely disheartening and a waste of the best resources of the nation. It is almost as disheartening and wasteful to keep a farm family in the tenant stage after it is ready to establish a farm home of its own.

Mortgage Encumbrance in Minnesota as Compared with That of Other States

A smaller proportion of the owner-operated farms in Minnesota in 1925 were mortgaged than in any neighboring states except Illinois (Table III). It had relatively fewer mortgaged farms than the aver-

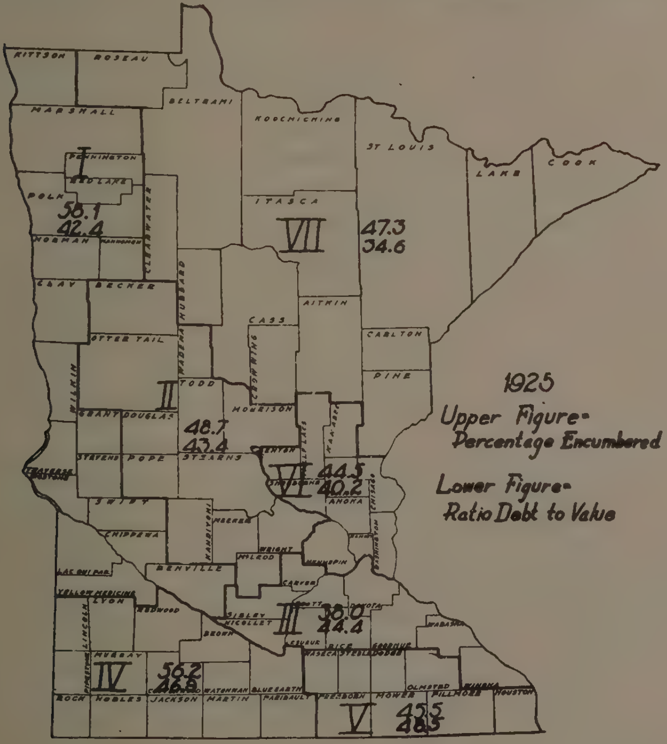

Fig. 7. Percentage of owner farms encumbered and ratio of debt to value of full owner mortgaged farms, by sections, 1925. The state is divided into 7 sections according to type of farming and other geographic conditions. These sections are designated as follows:

I	Northwest small grain section
II	Central small grain and dairy section
III	Southeastern small grain and dairy section
IV	Corn, small grain, hogs, and beef cattle section
V	Corn, small grain, and dairy section
VI	Potato, truck, and dairy section
VII	Cut-over section.

age of all the west north central states (Minnesota, Iowa, Missouri, North Dakota, South Dakota, Nebraska, and Kansas); but more than the average of all the east north central states (Wisconsin, Illinois, Michigan, Indiana, and Ohio). The figures indicate that the percentage of mortgaged farms in Minnesota decreased between 1920 and 1925 as in all neighboring states except South Dakota and Iowa. The percentage of mortgage indebtedness increased less between 1900 and 1920 than in all neighboring states except Iowa and Illinois. Between 1890 and 1900 the states west of Minnesota showed large decreases in the percentage of farms mortgaged; those to the east, small increases. Minnesota showed a small decrease. About the same comparison can be made as to ratio of debt to value of mortgaged farms. Iowa and Wisconsin had appreciably higher ratios than the rest of the group in 1925—Iowa, because of a spectacular increase, and Wisconsin, mostly because it always has been high. Iowa showed a much larger increase in the average size of mortgages between 1920 and 1925; and South Dakota and Illinois a somewhat larger increase.

It thus appears that Minnesota occupies an intermediate position between the east central and the west central states in most phases of mortgage encumbrance. Wisconsin has always had a great deal of mortgage encumbrance and very little tenancy. Many of its people came from countries of Europe where the ownership of small farms under mortgages has become an established arrangement. Also, its type of farming favors such a system of tenure. The Dakotas and Montana show the influence of being comparatively new regions with a relative scarcity of capital.

Distribution of Mortgage Indebtedness Within the State

This comparison with neighboring states helps us to understand conditions in different sections of Minnesota. The percentage of farmers in Minnesota reported encumbered and the ratio of debt to value, by sections, is given in Tables XVI and XVII for the census years from 1890 to 1925.

TABLE XVI

PERCENTAGE OF OWNED FARMS REPORTED ENCUMBERED, BY SECTIONS, IN MINNESOTA, 1890 TO 1920*

Section	1925	1920	1910	1900	1890
State	48.6	52.4	46.0	43.3	45.4
I	58.1	59.4	60.1	51.9	51.9
II	48.7	51.7	47.2	47.7	49.9
III	38.0	42.8	32.0	35.2	37.5
IV	56.2	59.3	56.2	55.0	53.5
V	45.5	48.9	40.7	38.9	46.1
VI	44.5	47.3	41.6	36.9	36.4
VII	47.3	54.3	37.1	16.4	17.6

* See Figure 7 for outline of sections.

Sections I and IV have a high percentage of farms mortgaged, like Iowa and eastern North and South Dakota. Section IV is much like Iowa in its mortgage encumbrance. Sections III, V, and VI resemble western Wisconsin rather than Wisconsin as a whole. Section VII, the new cut-over section, shows the same sort of increase in mortgage indebtedness that occurred in Montana and to a lesser extent in North Dakota. Previous to 1900 few farms in this section were sufficiently developed to warrant loans being made on them as security. After from 20 to 25 acres have been cleared and subdued, the farmer often wishes to borrow money in order to clear enough land to provide an income large enough that he need not work away from home. As his cleared acres increase, he needs better buildings, more dairy cows and machinery. For these reasons, the percentage of mortgaged farms grew rapidly in Section VII and by 1925 nearly equaled the average for the state.

TABLE XVII

RATIO OF DEBT TO VALUE OF MORTGAGED FARMS, BY SECTIONS, IN MINNESOTA, 1890 TO 1925

Section	Percentage of farm value mortgaged			
	1925	1920	1910	1890
State	43.6	27.5	26.4	31.6
I	42.4	25.4	25.6	32.5
II	43.4	28.9	25.8	31.5
III	44.4	29.2	27.8	33.0
IV	46.9	26.1	26.8	30.7
V	48.5	30.1	29.8	34.3
VI	40.2	28.4	24.7	25.2
VII	34.6	25.5	21.4	20.0

From 1920 to 1925 the percentage of farms mortgaged decreased in all sections of the state. The lowest decline was 1.3 per cent in Section I, where conditions are probably more stable than in any other area. The "land boom" of the post-war period is thought to have disturbed this area very little. The greatest reduction in the percentage of farms mortgaged was in Section VII, where it amounted to 7 per cent. The reduction in the other areas varies from 2 to 5 per cent. The explanation of this reduction has already been given. Some of the differences shown are probably due to the functioning of the credit mechanism.

All sections show an increase in the ratio of indebtedness to value on owner mortgaged farms. The smallest increase was 9.1 per cent in Section VII and the largest, 20.8 per cent in Section IV. Data for the various sections of the state as to changes between 1920 and 1925 in per cent mortgaged, value of farm land and buildings, and ratio of mortgage debt to value are given in Table XVIII.

TABLE XVIII

CHANGES IN PERCENTAGE MORTGAGED, VALUE OF LAND AND BUILDINGS, AND RATIO OF DEBT TO VALUE, MINNESOTA, BY SECTIONS, 1920 TO 1925

Section	Per cent mortgaged	Value of land and buildings	Ratio of debt to value
I	−1.3	−31.0	+17.0
II	−3.0	−25.3	+14.5
III	−4.8	−25.2	+14.2
IV	−3.1	−36.5	+20.8
V	−3.4	−25.1	+18.4
VI	−2.8	−15.3	+11.8
VII	−7.0	+10.8	+9.1

These data show that in Section VII the value of land and buildings increased 10.8 per cent, in other sections it decreased from 15 to 36 per cent. This explains why the ratio of debt to value in Section VII increased less than in other sections. The same relationship appears for the other areas, those with the largest decrease in land values having the largest increase in ratio of debt to value, and thus in order down to those with the smallest decrease in land values. The decrease was greatest after 1920 where land values increased most between 1915 and 1920 and where the mortgages were largest absolutely as well as relatively. As has been explained, the absolute increase in mortgage indebtedness shown in 1925 was largely due to the refunding into mortgage indebtedness of non-mortgage indebtedness contracted prior to 1920.

Geographic Comparison of Mortgage Encumbrance and Tenancy Combined

It will be remembered that when the value of rented farms was combined with the mortgage indebtedness to discover the value of farm real estate not owned by those who operate the farms, the percentage was 48.8 for Minnesota in 1925. This means that the operators of Minnesota farms own only 51.2 per cent of them. Similar data for 1890, 1910, 1920, and 1925 for Minnesota and neighboring states are given in Table XIX. This percentage has declined rapidly in all since 1910, less in Minnesota than in the Dakotas, but more than in Wisconsin and Illinois. In Minnesota, the Dakotas, and Wisconsin, the percentage was lower in 1890 than in 1910; in Illinois and Iowa, the decrease has been continuous since 1890. In Iowa, only a little more than a third of the land is really owned by those who operate it, and there was the startling decrease of 9.0 per cent between 1920 and 1925. In Minnesota the comparable decrease was 5.7 per cent; in South Dakota, 10.3 per cent.

CHANGES IN PERCENTAGE OF TENANCY FOR THE UNITED STATES, VARIOUS GROUPS OF STATES, AND FOR MINNESOTA AND NEIGHBORING STATES, 1880 TO 1925

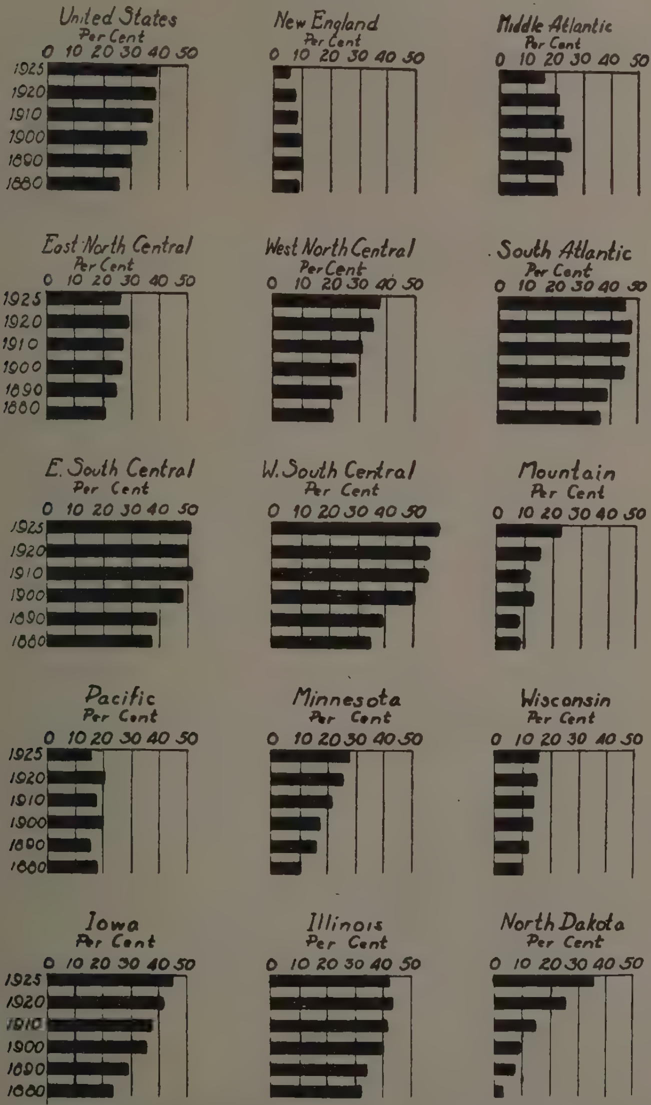

Fig. 8. In the period between 1910 and 1925, tenancy actually decreased in the New England and the Middle Atlantic states, and between 1920 and 1925 it decreased in the South Atlantic states. In the Atlantic Coast states as far south as Virginia, the recent tendency has been for tenancy to decline. Tenancy increased only 1.6 per cent in Wisconsin from 1910 to 1925 and only 0.6 per cent in Illinois, while it increased 6.1 per cent in Minnesota. During the same 15 years it increased 20.1 per cent in North Dakota. Between 1920 and 1925, tenancy in the United States increased only 0.5 per cent.

TABLE XIX

PERCENTAGE OF REAL ESTATE VALUES OWNED BY OPERATORS IN MINNESOTA AND NEIGHBORING STATES, 1890 TO 1925

Areas	1925	1920	1910	1890
Minnesota	51.2	56.9	65.5	51.9
North Dakota	50.5	56.4	72.1	69.1
South Dakota	43.1	53.4	63.2	59.6
Montana	57.2	64.7	72.5	86.7
Iowa	35.4	44.4	51.5	54.8
Wisconsin	57.5	61.5	66.0	65.5
Illinois	39.4	40.1	45.8	52.9

Progress of Individual Farmers

Altho the farm wealth of Minnesota and neighboring states is passing more and more into the hands of landlords and mortgage holders, the progress of individual owner-operators may not be so discouraging. Discussion of farmers' conditions in recent years has been too much in terms of those who bought land between 1918 and 1921. In the survey of 172 owner-operated farms made in the fall of 1924, 49 had bought farms between 1916 and 1921, and 36 before 1900. After deducting gains in gifts received since the time of purchase, all groups show a net gain except that of 1919-20, when land prices were at their highest (Table XX). Farmers who bought before the land boom all made substantial net gains and even those who bought after 1920 made some gain, on the average. Many of the older farmers, who purchased land in the earlier years, had prospered and sold out prior to the time of the survey. It is probable that those not included in the earlier periods because they had sold their farms previous to the survey would have shown a higher net gain than the average for those who continued to farm. On the other hand, numerous instances were related by farmers and bankers of individuals who had bought land at peak prices in 1919 and 1920, who had, prior to the survey, lost their farms, with whatever equity they had in them. The 1921-24 group in Table XX contains only 2 farms purchased in 1924, 2 in 1923, and 4 in 1922, leaving 11 purchased in 1921. Many of the farms bought in 1921 were purchased for considerably more than they would sell for in 1924.

The average net gains per farm for these 7 groups, after deducting gains from inheritance since purchase, were $14,751; $13,523; $11,255; $5,824; $6,297, —$89 and +$249. The large losses sustained by some in the last two groups were possible because these individuals had a considerable accumulation when they bought their farms. In many instances persons buying farms during the land boom period sold other farms at high prices just prior to their new purchase.

TABLE XX

NET GAINS OR LOSSES PER FARM, GROUPED ACCORDING TO TIME OF PURCHASE*

	1880-90	1891-1900	1901-10	1911-15	1916-18	1919-20	1921-24
No. of farms	11	26	35	32	21	28	19
Average acres per farm	211.3	151.3	188.3	138.8	138.6	110.0	114.7
Net assets per farm at purchase	$ 889	$ 1,118	$ 3,169	$ 4,813	$ 6,729	$7,690	$7,112
Net assets per farm in 1924	15,912	15,730	15,005	10,761	13,405	7,790	7,570
Gain in net worth from time of purchase to 1924	15,023	14,612	11,836	5,948	6,676	100	458
Gain from gifts	272	1,089	581	124	379	189	209
Smallest net gain or largest loss for any farm	5,375	3,025	3,050	1,865	1,100	−10,800	−8,960
Largest net gain for any farm	44,629	45,200	36,175	20,800	25,650	6,910	5,210

* Source of data, 1924 survey.

The survey farms are regrouped according to time of purchase in Table XXI. The second column of the table gives the number of owner-operated farms in each group. The rest of the table gives the relation of total liabilities to total assets at the time of the survey, in the following order: (1) the number of farmers having no liabilities, (2) the number whose total liabilities were respectively from 1 to 20 per cent, 21 to 40 per cent, 41 to 60 per cent, 61 to 80 per cent, and 81 to 100 per cent of their total assets. The data indicate two important conclusions: (1) that excessive debt is confined to farmers in the last three groups. Only one farmer among 104 who had bought farms before 1916 had debts amounting to more than 61 per cent of his assets, while 12 out of 68 who purchased farms after 1916 were indebted for more than 61 per cent and 6 for more than 81 per cent of their total assets. (2) Of the farm owners included in this survey, 3.5 per cent are near bankruptcy, and 4 per cent more probably do not have reserves sufficient to remain solvent if crops should fail for a year or two or if the price level for the products they have to sell should decline still lower for a considerable time.

The data given were taken four years after deflation set in, and in the meantime many farmers in Minnesota had gone bankrupt and many more had turned over their farms to their creditors without legal proceedings. An inquiry conducted by the United States Department of Agriculture in 1923 found that between 1920 and March, 1923, 4 per cent of the owner-farmers in fifteen corn and wheat producing states had lost their farms by foreclosure and 4.5 per cent more had let their farms go to creditors without legal proceedings.[8] This inquiry also found that the number of tenants who lost their savings was materially larger than the number of owners.

[8] The Year in Agriculture, 1923, by Henry C. Wallace. U.S. Dept. Agr. Yearbook, pp. 9-10.

TABLE XXI

Total Liabilities Compared with Total Assets, Farms Grouped by Periods of Purchase

Purchase periods	Total No. of farms	No. of farmers having indebtedness indicated					
		No debt	1-20 per cent	21-40 per cent	41-60 per cent	61-80 per cent	81-100 per cent
1881-90	11	7	4	0	0	0	0
1891-1900	26	17	8	1	0	0	0
1901-10	35	7	18	7	3	0	0
1911-15	32	9	9	10	3	1	0
1916-18	21	3	4	8	4	1	1
1919-20	28	4	5	7	6	2	4*
1921-24	19	1	2	9	3	3	1
Total	172	48	50	42	19	7	6
Per cent	100.0	28.0	29.0	24.5	11.0	4.0	3.5

* In one case the percentage of liabilities was 122.

The progress of the farmers with mortgages in 1924 and of the 172 owner-operators is analyzed in further detail in Table XXII. On the average, the mortgage indebtedness of the mortgaged group appears to have increased slightly, but the increase in farm values from $8,500 to $11,800 since purchase had more than offset this, so the percentage of debt had decreased from 55.7 to 40.3 per cent. For the whole group, both unencumbered and encumbered owners, the ratio of debt to value had decreased more than half. In due time, however, these owner-operators will retire or die and their farms will pass into the hands of new owners under heavier mortgages. This will probably keep the percentage of owners' equities from ever rising greatly. Even while this particular group has been reducing its ratio of debt to value from 49.7 to 23.3, new farmers have been buying farms under heavy mortgages, so the community average has probably been increasing.

TABLE XXII

Value and Debt at Purchase and in 1924 on Owner-Operated Farms in 1924 Survey

	Mortgaged owner-operated farms in 1924	All owner-operated farms
No. of farms	112	172
Value of real estate per farm		
At purchase	$ 8,500	$ 7,650
In 1924	$11,800	$12,600
Debt per farm at purchase	$ 4,700	$ 3,800
Mortgage debt per farm, fall of 1924	$ 4,800	$ 2,935
Percentage of debt at purchase	55.7	49.7
Percentage of mortgaged debt in 1924	40.3	23.3
Decrease in percentage of mortgage indebtedness by 1924	15.4	26.4

At the rate of payment of mortgage principal indicated in Table XXII, farmers will be a long time in getting out of debt. The increase in land values has increased their equities. It is sometimes urged that farmers should not worry about getting out of debt. Corporations do not worry greatly over their bonded debt so long as it is in reasonable proportion, and why should farmers worry over mortgage debt? One significant answer to this is that if each generation of farmers does not pay off a good part of its mortgage debt, and the farms continue to make their contribution to the city in the form of payments to retiring farmers and heirs to farm estates, it will be only a short time until all the land will be owned by landlords and mortgage holders. It is probable, however, that less farm wealth will be bequeathed to the city in the future, as smaller farm families mean fewer city heirs.

Sources of Long-term Loans

The principal sources of long-term loans used by Minnesota farmers are local banks, former owners of the land, the Federal Land Bank of St. Paul, Minnesota Rural Credit Bureau, retired farmers and other individuals, investment companies, life insurance companies, and joint stock land banks.[9] With the exception of the federal land banks, joint stock land banks, and the Minnesota Rural Credit Bureau, there are no satisfactory sources of data as to the volume of loans furnished by the various agencies. Table XXIII presents data gathered for small groups in six Minnesota counties in the fall of 1924. While the sample is small, the data probably show fairly well the relative importance of the principal sources. As might be expected, the largest volume of loans from any single source was from former owners of the land, with local banks ranking second. The former owners were supplying a little more than one fourth of the mortgage loans. No other source of long-term farm credit has been or probably could afford to be as liberal in assisting tenants with little credit or capital other than stock and machinery to become independent operators of their own farms. In Hubbard County, in the cut-over region, there are few retired farmers because of the relative newness of farming. Hence in this area less than one-tenth of the loans were from this source.

Retiring farmers often give credit for a large part of the selling price when disposing of their farms. It is not uncommon for the purchaser to make an initial payment of even less than 10 per cent of the purchase price. Sometimes a contract for deed is given and at other times the seller takes a mortgage on the farm. Another method, used when the seller wants considerable cash, is for the buyer to borrow as much as possible on a first mortgage and the seller to take a second mortgage for the unpaid balance. When land prices have gradually advanced for several years, owners are much more willing to sell with small payments down; when the land market is stagnant, it is often the only way a sale can be made. The plan usually works out well when prices of land are advancing, but when the farms have been purchased just preceding a great deflation, it has too often resulted in the loss of the invested capital.

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[9] By source is meant the person or institution that advances the money directly to the farmer and not the ultimate resting place of the loan.

TABLE XXIII

PERCENTAGE OF MORTGAGE LOANS ON OWNER FARMS FROM VARIOUS SOURCES, MINNESOTA, 1924

Source	Steele County	Cottonwood County	Polk County	Norman County	Chisago County	Hubbard County	All areas
	per cent	per cent	per cent	per cent	per cent	per cent	per cent
Local banks	31	8	14	23	28	26	21
Former owner	24	35	28	27	26	10	27
Federal banks	1	1	37	21	14	5	12
Joint stock land banks	0	5	6	1	1	4	3
Minnesota Rural Credit Bureau	0	15	1	6	18	43	10
Private and retired farmers	21	2	7	7	10	3	9
Investment company	3	20	1	6	2	7	8
Life insurance company	0	10	6	6	0	0	4
Relatives	20	4	0	3	1	2	6

Local banks were the source of about one-fifth of the owner-farmers' mortgage loans. This figure is probably too high, as in many cases the loans reported as obtained from banks were made by the banks as agents of insurance companies and investment companies. The farmers obtaining the loans did not know, in many cases, whether the bank made the loan directly or merely acted as agent. It is apparent that with the exception of the former owners of the land, farmers still go oftener to their local banks for mortgage loans than to any other one source. In some states, the state department of banking collects data on farm mortgage loans carried by state banks, but in Minnesota such data are not segregated for state banks. The total loans secured by farm real estate held by national banks in Minnesota as of June 30, 1925, amounted to $22,077,000.[10] We do not know how many loans were originally made to farmers and later sold; neither do we know how many were bought from a mortgagee or how many were on farms in other states or on rented farms. If the above sum was all on Minnesota farms, on the basis of a total estimated mortgage indebtedness of $495,569,400 as of January 1, 1925, the national banks held 4.5 per cent of the total. Reports of the comptroller do not show the amount of farm mortgage loans held by national banks in Minnesota in 1920. It has been estimated that 26 per cent of all loans were held by Minnesota banks in 1920.[11] The amount of loans carried by banks as invest-

[10] Report of comptroller of currency, 1925, p. 632.

[11] Farm Mortgage Loans by Banks, Insurance Companies, and Other Agencies, by V. N. Valgren and Elmer E. Engelbert. U.S. Dept. Agr. Bull. 1047, p. 3.

ments must not be confused with the amount originally made by them. Many of the loans they make are sold to insurance companies, to loan companies, to investment banks, and to an individual clientele.

The Federal Land Bank of St. Paul ranked third in importance as a source of farm loans in Minnesota and the Minnesota Rural Credit Bureau fourth. Practically all loans made by these institutions are on owner-operated farms. The joint stock land banks make some loans on rented farms. There is nothing to prevent an owned farm from becoming a rented farm after the loan is once closed. In the survey, the Federal Land Bank was found originally to have made 12 per cent and the Minnesota Rural Credit Bureau 10 per cent of the total volume of mortgage loans. The amount of net loans outstanding as of January 1, 1925, and January 1, 1920, for the Federal Land Bank of St. Paul, the joint stock land banks, and the Minnesota Rural Credit Bureau, together with the percentage that the outstanding amounts were of the estimated mortgage debt on all owner-operated farms is shown in Table XXIV. These percentages and the percentage of loans supplied by each of the three sources as found in the 1924 survey check rather closely. In the survey, the credit bureau was found to have supplied 10 per cent of the loans and the calculated figure is 9.3 per cent. After only two years of operation the Minnesota Rural Credit Bureau had loans outstanding equal to between 9 and 10 per cent of the total mortgage debt on owner-operated farms.

TABLE XXIV

NET LOAN OF FEDERAL FARM LOAN SYSTEM AND MINNESOTA RURAL CREDIT BUREAU IN MINNESOTA, 1920 AND 1925

	January 1, 1925		January 1, 1920	
	Volume	Mortgages on owner-operated farms	Volume	Mortgages on owner-operated farms
		per cent		per cent
Federal Land Bank of St. Paul. . .	$34,382,200	9.7	$14,607,900	4.6
Joint stock land banks.	33,748,339	9.5	5,953,600	1.9
Minnesota Rural Credit Bureau. .	32,296,148	9.3	*	*

* Not in operation. Organized in 1923.

The Federal Land Bank of St. Paul, on January 1, 1925, was supplying about 9.7 per cent of the mortgage loans on owner-operated farms and the four joint stock land banks about the same percentage (Table XXIV). Together they had outstanding about 19 per cent of the loans on owner-operated farms, as compared with 15 per cent as found by the survey. Part of this discrepancy is due to the fact that the federal land bank began loaning in 1917 and the joint stock land banks in 1919. In the meantime, some of the farms with federal farm loans had become rented farms, for which class mortgage data were not obtained in the survey. Moreover, joint stock land bank loans are sometimes originally made on rented farms. Together, the three institutions were supplying between 28 and 30 per cent of the mortgage loans on owner-operated farms on January 1, 1925. In 1920, they were supplying only 6.5 per cent.

TABLE XXV

Number and Amount of Loans Made, from Date of Organization to End of 1927, by Years

Year	Federal Land Bank of St. Paul			Joint stock land banks*			Minnesota Rural Credit Bureau†		
	No. of loans	Amount	Interest rate	No. of loans	Amount	Interest rate	No. of loans	Amount	Interest rate
			per cent			per cent			per cent
1927......	835	$4,940,800	5	116	$ 993,200	5½	971	$ 3,787,200	5¼
1926......	1,053	6,544,500	5	164	1,141,162	5¼-6	1,511	5,914,900	5¼
1922......	572	2,850,200	5-5½	618	5,440,010	5¼-6	1,317	6,144,200	5¼
1924......	737	4,284,500	5½	274	2,377,800	5½-6	5,338	27,590,400	5¼
1923......	1,324	6,696,500	5½	1,636	13,574,100	6	794	3,867,100	5¼
1922......	1,849	8.338.400	5½-6	1,451	13,685,750	6			
1921......	722	3,937,400	6	22	124,800	6			
1920......	615	3,616,400	5½	31	850,000	6			
1919......	1,430	5,921.700	5½	661	5,953,600	6			
1918......	1,478	4,792,900	5½						
1917......	869	1,164,500	5-5½						

* No report for loans in 1927 was received from the Des Moines Joint Stock Land Bank.
† Not organized until 1923.

The Federal Land Bank of St. Paul began operations in 1917. The first joint stock land bank operating in Minnesota was chartered in 1918 but transacted little business until the following year. Four more were chartered in 1919 and one in 1922. Two of these five joint stock land banks later combined with others so that at the beginning of 1927 there were but four operating in Minnesota.[12] The Minnesota Rural Credit Bureau was organized and began accepting applications for loans in the latter half of 1923. The annual number of loans and the volume of loans made from the time of organization to the end of 1927 by the foregoing organizations, together with the prevailing rate of interest, are shown in Table XXV. Both the federal land bank and the joint stock land banks loaned nearly 6 million dollars in 1919. The slump in loans made in 1920 and 1921 was due to the litigation then in process to determine the constitutionality of the federal farm loan act. The volume of loans made in 1922 and 1923 by the federal farm loan banks in Minnesota is the largest reached by them. This may be partly accounted for by the accumulation of applications from the two previous years. Their amortization plan of loaning and the relatively low interest rates charged were also factors. Other important factors were the shifting of loans from mortgage companies, owing to the great contraction of their market for loans among individuals, and also the considerable number of farmers who just at that time were funding their non-mortgage debts into mortgages. The large volume of loans made by the Minnesota Rural Credit Bureau in 1924 largely accounts for the reduced volume by the federal land bank and the joint stock land banks during that year. The volume of loans made by the Federal Land Bank of St. Paul in 1925 was lower than in any year since 1917. Conservatism and the desire to safeguard the institution from unsound loans may account for this. The investigation of joint stock land banks by the Treasury and the fact that one of the four banks operating in Minnesota was placed in receivership on July 1, 1927, may largely account for the low volume of loans made by them in 1927.

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[12] The four joint stock land banks operating in Minnesota were:
Southern Minnesota Joint Stock Land Bank, Redwood Falls, Minn.
Bankers Joint Stock Land Bank, Milwaukee, Wis.
Des Moines Joint Stock Land Bank, Des Moines, Iowa.
Minneapolis Joint Stock Land Bank, Minneapolis, Minn.

The Minnesota Rural Credit Bureau did a big business in 1924—made 5,338 loans and loaned $27,590,400. Great pressure for money was brought to bear through local banks in order to liquidate, so far as possible, their "frozen" loans to farmers. There was a reaction against this activity in the 1925 session of the state legislature. The law was revised and the bureau reorganized. From 1925 to 1927 less than 1,300 loans per year were made, as compared with over 5,000 in 1924.

The growth in the outstanding volume of loans in these new institutions has been continuous and pronounced. The Federal Land Bank of St. Paul, from the time of its organization to the end of 1927, made 11,484 loans and loaned $53,087,600. At the end of the tenth year of operation the number of loans outstanding was 2,844 less and the money outstanding was $9,469,800 less than the total loans to that date. This difference is due partly to the refunding of old loans into larger ones, partly to loans paid off, and partly to amortization payments. At the end of 1927, the joint stock land banks had made 4,973 loans representing $44,140,422. From 1923 to the end of 1927 the Minnesota Rural Credit Bureau had made 9,961 loans representing $47,303,800. The institutions are too new to make a safe prediction from the data at hand, but if not disturbed or curbed by legislative action, it seems probable that their business will continue to expand for several years.

Both the Federal Land Bank of St. Paul and the Minnesota Rural Credit Bureau have been less appreciated by the farmers in the southern tiers of counties in Minnesota than elsewhere in the state. Loans are available in the southern counties from other sources at nearly the same rates, especially from retired farmers and insurance companies. Besides, many farmers do not yet appreciate the amortization feature in farm loans. The Rural Credit Bureau has probably loaned more liberally in the cut-over section than has the Federal Land Bank of St. Paul. In Hubbard County, for example, 43 per cent of the total volume of loans among the farmers visited during the 1924 survey were obtained from the former as compared with about 9 per cent from the latter, including loans made by the joint stock land banks.

In both number and volume, and both absolutely and relatively to the total number and value of farms, the loans of the Minnesota Rural Credit Bureau have been larger in the northern and western counties than in the southern counties. (See Appendix, Table I.) The northern part of the state has been most discriminated against by the insurance companies. This is partly because the companies have regarded the loans in the southern part of the state as being more conservative, and partly because the loans per farmer are necessarily much smaller in the less developed sections of the state. The expense of examining the title and handling the management is as much for a $1,000 loan as for a $10,000 loan. In addition, the mineral and oil reservations commonly found in deeds to land in the cut-over section have been found objectionable to the insurance companies and also to some commercial loaning companies. In some cases, former deeds have reserved the right to repurchase the land for a stipulated sum in case oil or mineral is found on the land at any subsequent time. The federal land bank and the Minnesota Rural Credit Bureau are permitted under certain conditions to make loans to farmers having such titles to their farms. Loans may be made by the federal land banks on lands where oil, gas, and mineral rights have been reserved or leased, provided such lands are primarily agricultural. The land bank, however, inquires into the extent to which exercise of such rights may interfere with the use of the land for agricultural purposes and requires the borrower to include in his mortgage a statement of all his rights under such reservation and leases and an agreement to apply his royalties to the payment of the mortgage. Life insurance companies are still holding about twice as large a volume of farm loans in Minnesota as the federal and joint stock land banks combined. Life insurance companies are slowly taking up the idea of making amortized loans on farms. Their loans in Minnesota increased from $34,000,000 in 1914 to $116,000,000 in 1923. The financing of long-term loans by relatives and retired farmers is also relatively more important in the southern part of the state.

On January 1, 1925, the Minnesota Rural Credit Bureau, the Federal Land Bank of St. Paul, and joint stock land banks loaning on farms in Minnesota are estimated to have each held about 7 per cent of the estimated total mortgage indebtedness. National banks held 4.5 per cent, state banks 20 per cent, and insurance companies 27 per cent (Table XXVI). This accounts for the sources from which 72.1 per cent of the total mortgage indebtedness is obtained. It will be remembered that the total mortgage indebtedness on January 1, 1925, was estimated to be $495,569,400. Deducting the amount of mortgages held by the sources named, there remains $139,798,400 in mortgages to be held by former owners, retired farmers, and miscellaneous sources.

TABLE XXVI

ESTIMATED PERCENTAGE OF LONG-TERM MORTGAGE LOANS OBTAINED FROM SEVERAL SOURCES IN MINNESOTA

Date	Source	Amount	Percentage of total
Jan. 1, 1925	Minnesota Rural Credit Bureau	$ 32,296,000	6.5
Jan. 1, 1925	Federal Land Bank of St. Paul	34,382,000	6.9
June 30, 1925	National banks*	22,077,000	4.5
Jan. 1, 1925	Joint stock land banks	33,748,000	6.8
June 30, 1925	Insurance companies†	136,000,000	27.4
Jan. 1, 1925	State banks‡	99,268,000	20 0
	Total	$357,771,000	72.1

* Report of comptroller of the currency, 1925, p. 632.

† The amount held by national banks is known. It equals 4.7 per cent of the estimated total mortgage indebtedness. V. N. Valgren, in U.S. Dept. Agr. Bull. 1047, estimated in 1920 that all classes of banks in Minnesota held 26 per cent of the total amount of farm indebtedness. It is here assumed that the ratio is about the same in 1925. Deducting 4.7 per cent leaves 21.3 per cent to be held by state banks of all kinds. This method is used only for the lack of data for a better approach.

‡ Estimated actual for Dec. 31, 1923, was $116,496,565 as shown by report of association of life insurance presidents.

Data for the amount of loans held by the Minnesota Rural Credit Bureau, the Federal Land Bank of St. Paul, and the joint stock land banks are official and complete. In estimating the total debt it has been assumed that the value of part-owner farms bears the same relation to the indebtedness as that of full-owner farms. On the basis of a survey made in 1920, the United States Bureau of Agricultural Economics estimated that tenant farms in Minnesota were mortgaged for 11.7 per cent of their value. It has here been assumed that the ratio of debt to value on tenant farms changed after 1920 to the same degree as it did on owner farms. The insurance company figure is estimated from the amount of loans outstanding on January 1, 1924, it being assumed that the rate of increase in 1924 was the same as during the previous year.

The foregoing discussion of the principal sources of farm mortgage loans leads to the conclusion that comparatively few farmers are fully acquainted with the advantages of the long-term amortization type of loan. The improvements and the farm itself are investments of such a nature that the returns from them are spread over many years. When interest rates are generally low, farmers are able, especially in the older communities, to obtain local money from private sources at a rate of interest as low as that offered by the Minnesota Rural Credit Bureau or the Federal Land Bank of St. Paul, or even lower. However, most of these local loans are for five years or less and may need to be renewed at a time when interest rates are high, and perhaps when, owing to money stringency, it may be difficult to borrow from new sources. At such a time institutions are usually able to make only a small percentage of the loans demanded. It seems reasonable to suppose that if the majority of farmers had their loans on an amortization basis, some of the hardships caused by a money stringency might be eliminated. Even if rates are not higher when the short term loans mature, there is in most cases a renewal expense to pay at the end of each five years until the loan is liquidated. With the amortization loan, there are no renewal expenses. The farmer, instead of the lender, occupies the preferred position. If he wishes to pay off all his loan or any part of it in or after five years, or pay more rapidly than the contract calls for, he may but can not be compelled to do so. If interest rates have risen, he continues to pay at the old rate. If they have declined, he may pay off his old loan and take out a new one.

The farmer may get application blanks on which to apply for a state loan from the county auditor of the county in which he lives. In the case of the Federal Land Bank of St. Paul, the farmers have organized national farm loan associations in all parts of the state to handle co-operatively the mortgage needs of its members. National farm loan associations are fairly well distributed over the entire state, so that some association is within the reach of every farmer (Fig. 9).

Second Mortgage Loans

The second mortgage obligations found among the farmers included in the Minnesota survey were provided for as follows: Commercial banks, 61.5 per cent; retired farmers and relatives, 15.4 per cent; investment companies, 7.7 per cent. No special institutions have been developed in Minnesota or elsewhere to handle second mortgages. The specialized first-mortgage loaning agencies are performing a splendid service for the man who has capital or additional credit to finance 50 per cent of the value of his land and 80 per cent of the value of his buildings. Evidently many will remain tenants until late in life if they must wait until they are able to finance themselves to this extent. As land values become stabilized and more accurate methods of farm appraisal are worked out and used by loaning agencies, society may safely provide means of financing tenants for a very much higher percentage of farm values. The risk on second mortgages is higher, and the rate charged should be sufficient to cover the additional risk. The same general organizations might provide the second mortgage facilities, but the means and method of financing should be entirely separate.

Commission mortgages were formerly common in Minnesota. Before present marketing facilities for farm loans were provided, local brokers waxed fat on commission mortgages taken from farmers as pay for securing a market for their mortgage loans. If the rates charged the farmers were 7 to 10 per cent, a first mortgage was often

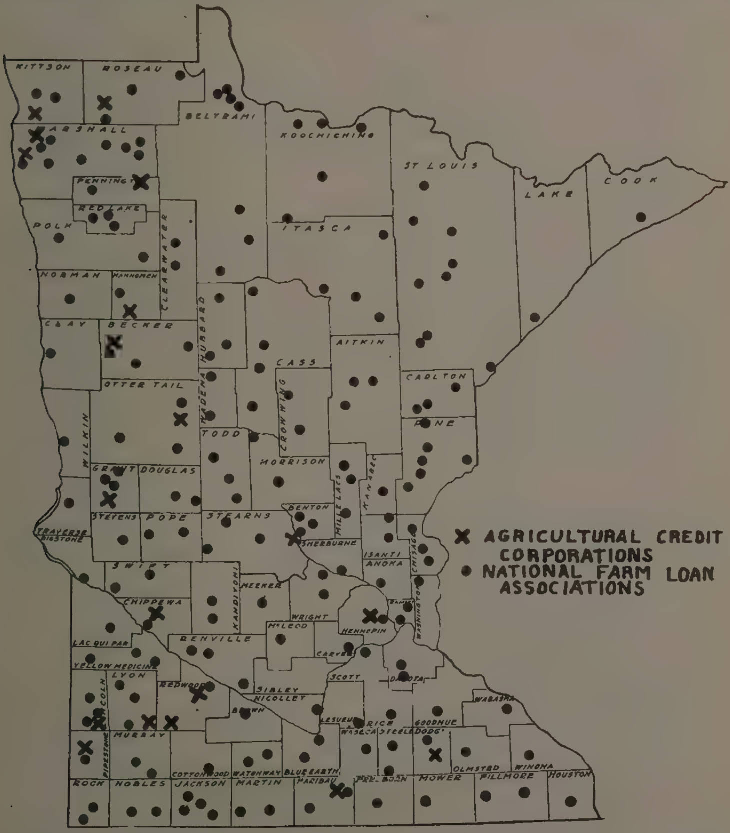

Fig. 9. Distribution of Agricultural Credit Corporations and National Farm Loan Associations in Minnesota on April 1, 1926. (Data supplied by Federal Land Bank of St. Paul.)

drawn and sold at 6 per cent interest, and a commission mortgage or second mortgage payable yearly in amounts equal to from 1 to 4 per cent of the face of the loan was taken as pay for the services of the broker. The margins taken on commission mortgages tend to be less now than before the advent of special credit institutions, and usually the local brokers' services are paid as a cash fee, which is deducted at the time of final settlement with the farmer. This seems to be a more business-like way of paying for the service than the commission mortgage.

Mortgage Interest Rates

The 1920 census contained an inquiry as to the interest rates paid on farm mortgages by owner operators. Figure 10 gives the results as county averages. The range is from 5.0 per cent in Carver County to 7.1 per cent in Koochiching County. The rates are, in general.

MORTGAGE INTEREST RATES IN 1920, BY COUNTIES

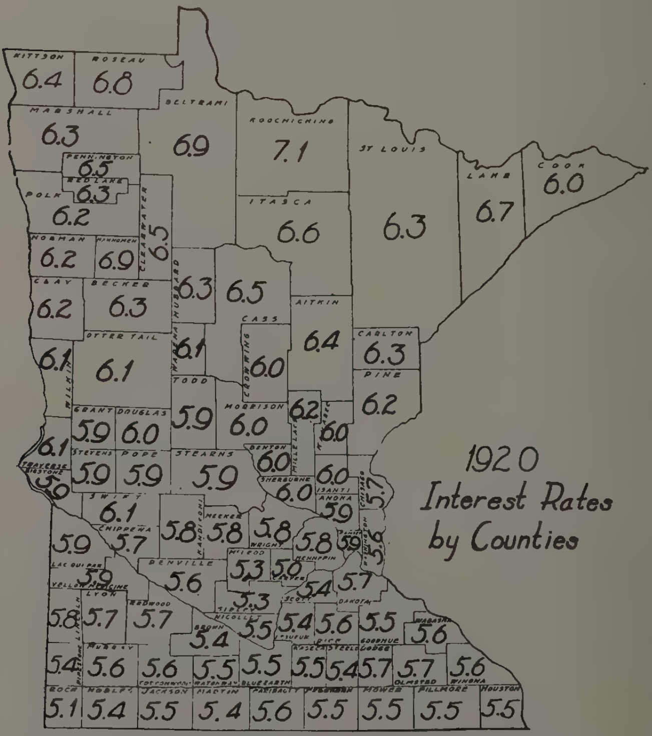

Fig. 10. The interest rates ranged from 5 per cent in Carver County to 7.1 per cent in Koochiching County. In general, rates are lowest in the counties west and south of the Twin Cities and highest in the counties north and northwest.

lowest in the counties west and south of the Twin Cities, and highest in the counties north and northwest. Figure 11 gives these rates and also the rates in 1890 according to the nine districts into which the state is divided for crop reporting purposes by the United States Department of Agriculture. The decrease for the state in this 30-year period is 2.6 per cent, ranging from 2.0 per cent in District 9 to 3.2 in District 2. (The 1890 rate for District 3 could have represented only the immediate vicinity of Duluth.) Farm mortgage interest rates tend to be low near the larger cities. In 1890, capital for farm development was very scarce in Minnesota. No census of interest rates was taken between 1890 and 1920. The rate of interest charged by banks on farm mortgages in 1920 was one per cent higher than the average rates for farm mortgage loans from all sources. Loans from relatives, former

MORTGAGE INTEREST RATES IN 1890 AND 1920, BY CROP REPORTING DISTRICTS

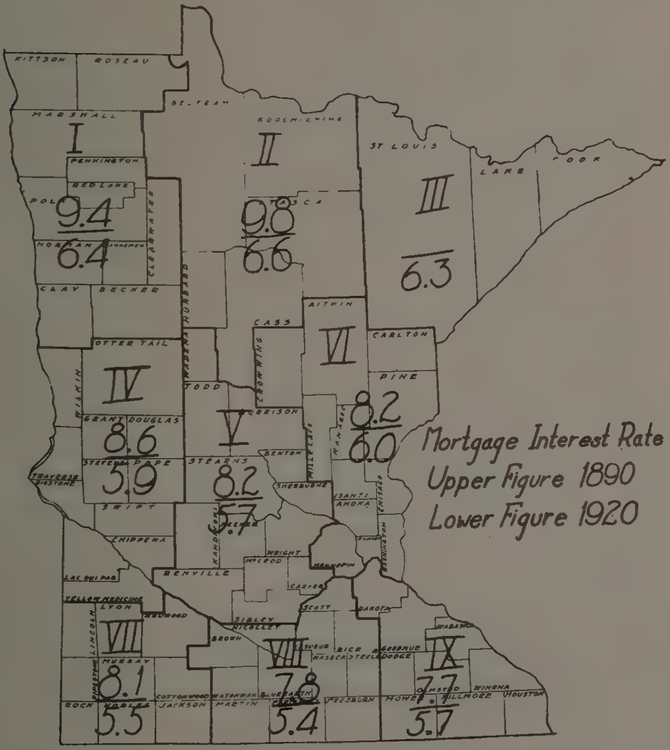

Fig. 11. The average decrease in interest rates for the state in the 30-year period was 2.6 per cent, ranging from 2.0 per cent in District I to 3.2 per cent in District II.

owners, and retired farmers tend to be at lower rates than loans from local banks. Loans from public agencies have also been at lower rates than from local banks, in many parts of the state. The banker's rates declined about one per cent, on the average, from 1921 to 1926, the decline ranging from 2.6 per cent in District 7 to 0.5 per cent in District 6 (Table XXVII). If the average rate for mortgage loans from all sources declined in the same proportion, a census taken in 1926 would have shown a state average of 5.2 per cent. Probably other rates declined less than banker's rates.

TABLE XXVII

INTEREST RATES ON FARM MORTGAGES IN MINNESOTA; ALL FARM MORTGAGES IN 1920; LOCAL BANK MORTGAGES, 1921 AND 1926

Districts	1920 census all farm mortgages	Local bank mortgage loans	
		1921	1926
	per cent	per cent	per cent
1	6.4	7.0	6.3
2	6.6	8.1	7.3
3	6.3	8.0	7.0
4	5.9	6.5	5.4
5	5.7	6.3	5.6
6	6.0	6.7	6.2
7	5.5	7.6	5.0
8	5.4	6.2	5.4
9	5.7	6.1	5.5
State	5.8	6.8	5.9

Rates in the cut-over section are surprisingly low. This is because land companies selling cut-over land furnish most of the credit. Studies of farms in northern Minnesota made by the Division of Agricultural Economics in 1919 and 1920 contain reports of 296 purchases on contract at an average interest rate of 6.1 per cent, and 161 purchases on mortgages at 6.5 per cent interest. But the rates on farm mortgage loans from local banks averaged 7.4 per cent. The land companies find it easier to ask $5 or $10 extra per acre for land than to ask 7 or 8 per cent interest on mortgages—$25 to $30 an acre for used land seems not half so unreasonable to a buyer from Illinois as 7 or 8 per cent interest on a loan, and yet it amounts to about the same.

There are good reasons for assuming that the activities of the new sources of loans have lowered the interest rate on farm mortgages. (1) Federal land banks have standardized farm mortgages. The federal appraisers, presumably, are not influenced by local considerations. Mortgages are deposited as security for bonds, which are instrumentalities of the government and for which the twelve banks are jointly liable.[13] (2) The market for mortgage bonds has been broadened.

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[13] The government does not guarantee these bonds, but being instrumentalities of the government they are tax free.

Bonds are now issued in denominations as low as $40. The bonds are suitable investments for savings banks, and are eligible as security for deposits of government funds. Further, the income from farm loan bonds is exempt from federal, state, and local taxation.

There is also some statistical evidence that federal land banks have lowered interest rates paid by farmers on mortgages. The margin between the rates charged by savings banks on first mortgage farm loans in Minnesota and the average rates earned by ten high-grade railroad bonds and the average rate on prime commercial paper, is less now than before the federal land bank began operating (Fig. 12). The activity of the federal land bank in Minnesota is probably one of the factors affecting this change. Another factor is the decreasing risk in connection with farm loans as farm communities are developed. Since 1920, the market outlets for farm loans through farm mortgage companies have been demoralized. The Federal Land Bank of St. Paul

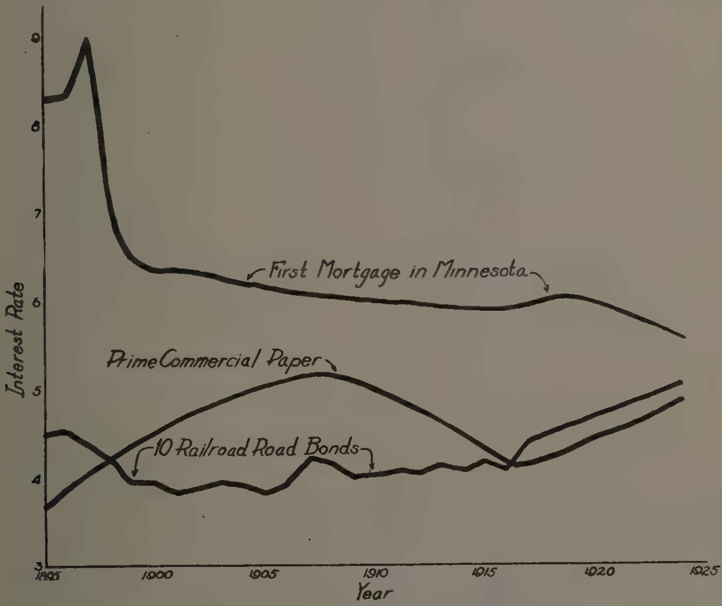

Fig. 12. Curves showing rates charged by savings banks on first mortgage farm loans, the average rates earned by ten high grade railroad bonds, and the average rate on prime commercial paper from 1895 to 1924.

and the Minnesota Rural Credit Bureau probably have lowered the rate of interest that Minnesota farmers would otherwise have paid for loans between 1920 and 1927.

The rate charged by savings banks does not tell what the farmer had to pay for money, but rather the rate at which the broker of farm mortgages could sell them. If money in the community was plentiful, the broker usually worked on a narrow margin. If not, he often charged all the traffic would bear. Another source of gain to the farmer from federal land banks is the savings on margins and commissions formerly taken by the local brokers of farm mortgages, and the elimination of the expense of frequent renewals. No commissions are charged on loans made under the farm loan act and the interest can not exceed 6 per cent. At present the interest rate charged by the Federal Land Bank of St. Paul is 5 per cent. Farmers having loans made when the interest rate was 5.5 and 6 per cent may liquidate them by taking a new loan at the lower rate of interest when the old loans have run five years.

The federal farm loan banks on January 1, 1927, had $1,077,858,723 outstanding to the farmers of the United States on real estate security. Even if the saving to the farmers in interest and commissions is assumed to be but 0.5 per cent, which is a most conservative estimate, this would amount to an annual saving of over 5 million dollars. If the level of rates on loans from other sources has also been lowered, this will represent a vastly larger saving.

The loans in Minnesota of the Federal Land Bank of St. Paul and of the Minnesota Rural Credit Bureau on January 1, 1927, amounted to $81,194,800. Assuming the same average saving of 0.5, these institutions are saving the farmers of Minnesota annually $406,000 just on the money loaned by them. A saving of 0.5 per cent on the total estimated mortgage indebtedness on Minnesota farms on January 1, 1925, would amount to an annual saving to the farmers of 2⅓ million dollars.

SHORT-TERM CREDIT

Short-term credit is here defined as credit for a year or less, because a majority of the short-term loans made to farmers in Minnesota are for a longer period than six months, the usual upper limit named for a strictly short-term loan. Such a limit is far better suited to commercial than to agricultural loans. The principal sources of such credit are country banks, stores, and private individuals, the country bank being by far the most important source.

In this section, short-term credit will be considered under two heads, that secured by personal notes or chattel mortgages, called personal or collateral loans, and that provided by merchants, called mercantile credit. Usually, when collateral or personal cash loans are made the intention is to repay the principal at the end of a period not exceeding one year. These loans are often continued by renewals for an indefinite time. After a period of prosperity in which farmers have been encouraged by business men and bankers to extend their credit, an abnormal proportion of these short-term loans become a part of the fixed indebtedness and eventually are incorporated with the mortgage indebtedness. Credit at mercantile establishments for more than 30 days is here considered as mercantile credit.

As already explained, little information is available as to short-term credit. What is here presented is mostly obtained from the survey made in the six Minnesota areas in 1924.

TABLE XXVIII

COLLATERAL AND PERSONAL LOANS FROM SURVEY OF 6 MINNESOTA AREAS, 1924

County	Area No.	Tenants	Owner-operators	Both
A. Percentage Borrowing				
Steele	1	40	47	46
Cottonwood	2	85	46	72
Pope	3	40	37	38
Norman	4	47	50	49
Chisago	5	..	42	..
Hubbard	6	..	45	..
Average		61	44	49
B. Average Amount per Debtor				
Steele	1	$1,488	$1,444	$1,453
Cottonwood	2	1,735	1,747	1,737
Pope	3	1,024	1,199	1,152
Norman	4	1,340	1,388	1,360
Chisago	5	....	1,032	....
Hubbard	6	....	389	....
Average		1,581	1,143	1,294
C. Average for the Class				
Steele	1	$ 577	$ 700	$ 670
Cottonwood	2	1,488	780	1,258
Pope	3	480	352	384
Norman	4	657	1,028	848
Chisago	5	....	430	....
Hubbard	6	....	175	....
Average		958	505	631

Sixty-one per cent of tenants and 44 per cent of owner-operators were using short-term credit in 1924 (Table XXVIII). A greater frequency of collateral loans among tenants would be expected, especially after a period of depression in farm prices, as tenants have no opportunity to convert credit obligations contracted in a period of prosperity into long-term farm mortgage loans. The average amount owed by all farmers of the indebted class was $1,294 per person, and the average for both debtors and those not so indebted was $631. The average amount per debtor for farm owners was $1,143 and for tenants $1,581. Apparently, the tenants in Area 2 were the most heavily involved. The indebtedness per farmer in the various areas is not strictly comparable, as in the wheat region a considerable portion of the grain crop had been marketed and the proceeds applied to reduce indebtedness, while in the corn and hog areas, many hogs had not been marketed at the time the survey was taken. A few tenants in Area 1 had borrowed in order to purchase feeders, which would increase their indebtedness. The farmers in Areas 1 and 4 depend less on dairying than those in the other areas, and dairying was relatively profitable from 1921 to 1923. The average personal cash loan for all tenants was $958, for all owner-operators $505, and for tenants and owner-operators, $631.

TABLE XXIX

PERCENTAGE OF PERSONAL OR COLLATERAL LOANS FOR VARIOUS PURPOSES IN SIX AREAS OF MINNESOTA

Purposes	Steele County, Area 1	Cottonwood County, Area 2	Pope County, Area 3	Norman County, Area 4	Chisago County, Area 5	Hubbard County, Area 6	Average for all areas
			Owners				
Land	65	0	19	42	45	32	40.0
Buildings and improvements	25.5	91	20	0	29	24	27.0
Equipment and machinery	3.5	..	7	15	10	6	7.5
Livestock	3.5	..	7	..	1	5	2.0
Operating expenses	1.5	9	39	43	10	26	21.0
Miscellaneous*	1	..	8	..	5	7	2.5
			Tenants				
Rent	10	..	5	16	..	..	5
Equipment and machinery	33	45	33	51	..	..	44
Livestock	50	46	33	21	..	..	40
Operating expenses	7	3	3	7	..	..	4
Miscellaneous*	..	6	26	5	..	..	7

* Under miscellaneous are such items as school, sickness, bank stock, and automobiles.

Purpose of Short-Term Loans

In the six areas surveyed, 40 per cent of all collateral and personal loans was for financing land purchases (Table XXIX). Two classes of people make up the bulk of those borrowing on short-term notes in order to purchase land: (1) The successful farmer out of debt who wishes to buy a small adjoining tract; and (2) the farmer who is related to the person from whom the land is bought. Such notes are usually renewed from year to year until paid. Loans for buildings and other improvements come next and then operating expenses. One of the items frequently mentioned under operating expenses is labor for seasonal work. Farmers complained that the wages they were compelled to pay to harvest the crop at the right time were too high when compared with the selling price of the crop. The fact that some tenants were compelled to borrow money with which to pay their rent may suggest that some rents were still too high for the prevailing farm price level. It may have been due to dependence mostly upon one crop, which failed. Most of the tenants owed considerably more on their livestock, machinery, and equipment than the owners and were not far along the road to ownership. Tenants ordinarily borrowed more for living expenses than owners, many having started the year without reserves.

Security

Table XXX indicates that bankers and others who loan money to farmers for short and intermediate periods are not too particular about security. When 70 per cent of the owners and 38 per cent of the tenants can borrow money without pledging any definite property in payment of the debt, they enjoy a very high credit rating. The forms of security required in Minnesota are limited. The practice of having a neighbor sign a note with the borrower was generally unpopular. Usually, either a plain note is accepted or a note secured by a chattel mortgage on livestock, machinery, or other equipment. The consensus of opinion among bankers interviewed seemed to be that losses had been considerably less from small unsecured loans than from large secured loans. More information is needed as to the cost of the risk on loans to various classes of farmers and in different systems of farming. It may be socially desirable to underwrite such risks by adding the cost to the interest rate. If so, it would be necessary to spread the cost over a wide territory. Careful investigation in this field might lead to social and economic gains and increase individual opportunities.

TABLE XXX

SECURITY FOR PERSONAL OR COLLATERAL LOANS, 1924 SURVEY

Form	Owners	Tenants
Farmer's note	70	38
Chattel security	28	54
Plain note plus one signer	1	4
Plain note plus two signers	1	..

Need for Better Bank Loan Practices

Generally, the country banks of Minnesota have taken pride in assisting the farmers to promote their business. During the period of rising prices, from 1897 to 1920, bankers generally were assiduous in fostering cordial relationships with the farmers. This is desirable. But people who find themselves beginning to prosper often borrow or buy on credit too freely for their own good. Bankers should be better informed on the agricultural situation. Many bankers make loans to farmers in order that they may plant more wheat or buy more cows or sheep, when a knowledge of production trends and price levels would dictate exactly the opposite policy.

A better business relationship would be developed if bankers would compel each farmer to make a financial statement before loaning to him, and if they would more carefully analyze the purposes for which he wishes to borrow. The financial statements now required by the federal reserve banks and the intermediate credit banks before farm paper will be discounted, are satisfactory and should be used by all country banks. The old system, under which the banker took a pleasant drive through the country during the summer, getting a bird's-eye view of the farms and the condition of the crops and livestock, and then loaned liberally the balance of the season, if conditions looked good to him, must give way to risk analysis as a basis for sound investment.

Period of Collateral or Personal Loans

More than half of the collateral and personal loans to both farm owners and tenants in these areas were drawn for from nine months to a year. Only 25 and 31 per cent, respectively, were due in six months, and only 7 and one per cent, respectively, in less than 90 days (Table XXXI). Such loans are often too large to be paid from current earnings. A survey of country banks would probably show that the conventional banking theory that country banks can not safely make loans to farmers for more than six months does not conform to practice. Bankers are more interested in having ample assets back of their loans than they are in having all their loans paid at maturity. In a panic period, however, when deposits are declining, the effect of having a considerable portion of the bank's assets in comparatively long-term paper is often a shortage of funds for meeting the demand of current loans. Bankers are prone to forget this in prosperous times. Since the federal reserve system has been created, loans having sufficient security that they can be rediscounted may be of more importance than the length of time for which the loan is made. The country bankers' problem of a money reserve has been greatly simplified since the federal reserve banks began mobilizing the liquid reserves of the country. Dairying and diversified farming in Minnesota have further simplified the short-term credit problem for both the farmer and the banker. Further diversification will help still more. Where there is a steady flow of income as distinguished from the "after harvest" settlement, as with the general grain farmer, it ought to be feasible to operate short-term loans on the basis of from three to six months.

TABLE XXXI

Period of Collateral and Personal Loans in Six Areas Surveyed

Period	Owners, per cent	Tenants, per cent
60 days or less	1	..
90 days	6	1
6 months	25	31
9 months to a year	54	57
More than a year	5	..
Indefinite	9	11

Mercantile Credit

Few Minnesota farmers use much store credit. The practice of merchants "grub staking" the farmers during the planting, harvesting, and marketing of the annual crop seems to be rapidly disappearing. Only 13 per cent of the owner operators and 17 per cent of the tenants were using such credit (Table XXXII). In North Carolina, Georgia, and Tennessee, where farmers generally can not obtain funds from banks, mercantile credit is used very extensively. Surveys in Georgia in 1923 found 100 per cent of the farm owners using mercantile credit and from 30 to 50 per cent of owners and tenants combined.[14] The relative volume of mercantile credit in Minnesota is less than one per cent of the total farm debt, being a matter of convenience rather than another method of borrowing. Mercantile credit is used to a greater extent in new sections of the state and in one-crop sections than in the older and diversified sections. In a few instances farmers were getting 5 per cent discount for cash. There seems to be a slight tendency in this direction.

TABLE XXXII

Amount of Mercantile Credit in Six Areas Surveyed

County	Area	Owners		Tenants	
		Percentage using such credit	Amount per borrower	Percentage using such credit	Amount per borrower
Steele	1	10	$296	30	$106
Cottonwood	2	7	150	18	234
Pope	3	0	0	10	20
Norman	4	20	242	10	350
Chisago	5	23	170	..	...
Hubbard	6	15	120	..	...
Average	All	13	$189	17	$169

The rate of interest on mercantile credit is rather indefinite. If interest was charged, it was usually 8 per cent. Many farmers were carried without interest for a few months by hardware dealers, lumber dealers, general merchandise dealers, and doctors. Merchants of the South often charge tenants from 30 to 40 per cent for credit, and the average rate charged in North Carolina in 1922 was 26 per cent.[15] Mercantile credit is usually carried as an open account, and except in the case of farm machinery, where a conditional sales contract is often used, no particular security is pledged. Crop liens are practically unknown in connection with mercantile credit in Minnesota.

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[14] Farm Credit, Farm Tenancy, and Farm Taxation, by Nils A. Olsen, C. O. Brannen, G. F. Cadish, and R. W. Newton, U.S. Dept. Agr. Yearbook, p. 229.

The high concentration of the use made of mercantile credit, as shown in Table XXXIII, is significant. Fifty per cent of mercantile credit extended to farm owners is used for rather durable additions to the farm capital—building material and machinery. Tenants still have the hardware stores to aid them in obtaining the machinery necessary to operate their farms. Of their mercantile credit, 71 per cent was for hardware and implements.

TABLE XXXIII

PURPOSES SERVED BY MERCHANT CREDIT IN SIX AREAS STUDIED

Owner-Operators	Per cent
Implements and hardware	31
Food and clothing	61
Building material	19
Miscellaneous	4
Tenants	
Implements and hardware	71
Garage bills	26
Miscellaneous	3

Fewer of either owners or tenants were using the merchant as a source of credit than we have been accustomed to expect. This indicates that the practice of paying cash for groceries and supplies is becoming common. Only one owner operator out of eight and one tenant out of six were using store credit. Several farmers and merchants said that the use of credit for buying feed and supplies declined rapidly after 1920, principally because:

1. Credit extended by wholesale houses to merchants was restricted after 1920, compelling the merchant, in turn, to restrict the amount of credit extended to farmers.

2. Competition of cash-and-carry stores and of mail-order houses has compelled more merchants to mark their goods on a cash-sale basis.

3. As farmers generally milk a few cows, they are able, like their city friends who receive a regular income, to pay their bills at the end of each month. In many cases, however, the farmer pays every two weeks, as the cream checks are received.

[15] Farm Credit in North Carolina, by Fred R. Yoder, H. S. Beachley, and A. J. Honeycutt, Bull. North Carolina Dept. of Agr., p. 24, Raleigh.

To farmers who are buying lumber, machinery, and supplies on credit, the suggestion is made that it probably would be better to discontinue this practice and make a greater use of banks. Merchants who sell for cash should be able to sell more cheaply than those who extend credit freely. Experience has proved that mercantile credit is more expensive than bank credit. The advice is not to use more credit, but to purchase credit where it is the cheapest.

Interest Rates on Short-Term Credit

The latest published information on rates of interest on short-term loans in Minnesota is for 1916.[16] In Figure 13, interest rates in 1916 are summarized by crop reporting districts. The rates ranged from 6.9 per cent in District 9 to 11.4 per cent in District 2. They average about 2.5 per cent higher than the interest rates on farm mortgages

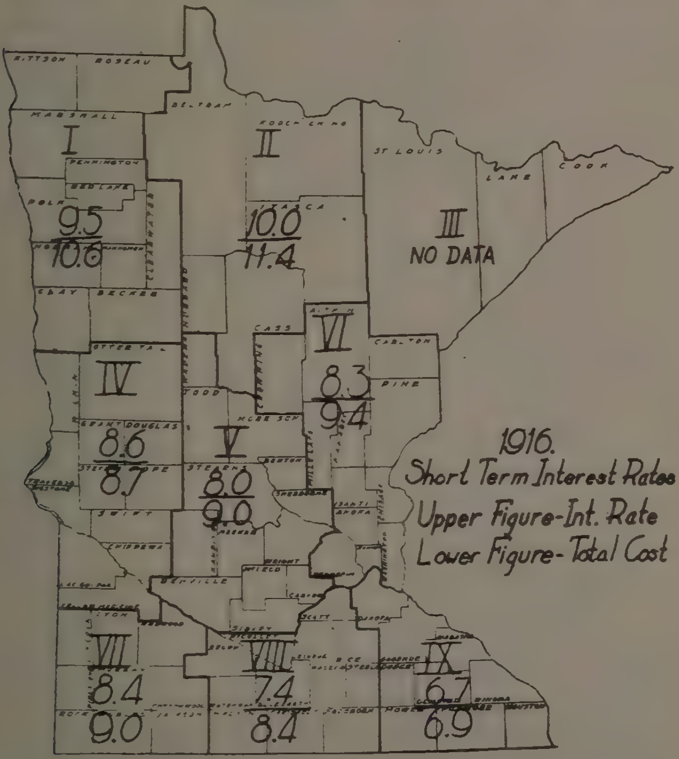

Fig. 13. Short-Term Interest Rates in Minnesota by Crop Reporting Districts, 1916

in 1920. The difference is in about the same proportion in the various districts except Districts 1 and 2, where the mortgage loans average 3.2 per cent higher, while in District 9, in the southern part of the state, the spread is only one per cent. As already explained, mortgage rates are surprisingly low in the cut-over region because land companies furnish so much of the credit. The comparison really should be with the bankers' rates on farm mortgages, which were probably about 6.6 per cent in 1920. Scarcity of capital is no doubt a factor in the higher rate in some parts of the state, but more important factors are the greater risks associated with loans in small-grain and new regions, and the higher unit costs of operating the smaller banks found in some of these areas. Rates also tend to be higher on small loans.

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[16] Factors Affecting Interest Rates and Other Charges on Short-Time Loans, by C. R. Thompson, U.S. Dept. Agr. Bull. 409, p. 4. Rates quoted are the average total cost of loans including discounts, bonuses, and other extra charges, as reported by correspondents.

TABLE XXXIV

PERCENTAGE OF SHORT-TERM LOANS MADE AT THE VARIOUS RATES OF INTEREST; 1924 SURVEY

County	Interest rates to owners, per cent							Rates to tenants, per cent			
	4	5	5½	6	7	7½	8	5	6	8	10
				Borrowed from Banks							
Steele	..	..	..	..	..	..	100	..	..	100	..
Cottonwood	..	..	..	20	..	..	80	..	6	94	..
Pope	..	..	..	..	..	..	100	..	..	100	..
Norman	..	..	..	8	..	8	84	..	..	100	..
Chisago	..	..	..	..	47	7	46	..	..	..	..
Hubbard	..	..	..	..	..	..	100	..	..	..	..
				Borrowed from Private Individuals							
Steele	..	14	15	71	..	..	..	..	100	..	..
Cottonwood	..	..	..	..	..	..	..	100	..	..	..
Pope	..	..	..	..	..	..	..	..	..	..	..
Norman	..	..	..	..	..	..	..	..	100	..	..
Chisago	100	..	..	..	..	..	..	..	..	..	..
Hubbard	100	..	..	..	..	..	..	..	..	..	..
				Borrowed from Relatives							
Steele	75	25	..	..	..	..	..	..	..	..	..
Cottonwood	..	100	..	..	..	..	..	..	..	..	..
Pope	..	..	..	..	..	..	..	..	..	..	..
Norman	100	100	..	..	..	..	..	..	..	..	..
Chisago	100	..	..	..	..	..	..	..	..	..	..
Hubbard	..	..	..	100	..	..	..	..	..	..	..

All other sources at 8 per cent except one loan at 6½ per cent.

The most recent data available on short-term interest rates in various sections of Minnesota are those obtained in the 1924 survey. The rates reported by the borrowers were lowest from relatives, highest from banks, and between the two from private individuals (Table XXXIV). The data show a general tendency for banks in all parts of the state to charge local farmers the maximum legal rate of interest.[17] One reason for this is that since 1920 country banking has not been profitable. All bankers agree that higher rates are needed. In Steele, Pope, and

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[17] The legislature of 1923 changed the maximum legal rate from 10 to 8 per cent.

Hubbard Counties, all owner-farmers interviewed said they were paying 8 per cent interest; likewise the tenants in Steele, Pope, and Norman Counties. Only 6 per cent of the tenants in Cottonwood County enjoyed a bank rate of less than 8 per cent. For all areas combined, the owners were paying interest at the following rates:

85.0 per cent were paying 8.0 per cent.
2.5 ” ” ” ” 7.5 ” ”
7.8 ” ” ” ” 7.0 ” ”
4.7 ” ” ” ” 6.0 ” ”

The interest rate on the bulk of the loans to owners from private parties and from relatives was from 4 to 5 per cent; to tenants, more often 5 and 6 per cent. Since 1924, there probably has been some reduction in interest rates, especially in the southern counties. Banks are being consolidated and in some cases liquidated. On January 1, 1926, there were 302 fewer banks in Minnesota than on January 1, 1920. Unless a local monopoly rate prevails, rates on short-term notes may be expected to decline somewhat from the level of 1924.

Short-Term Credit in Cut-Over Areas

The special study made of settlement conditions in northern Minnesota and the neighboring cut-over area in 1919 and 1920 brought out important facts relative to short-term loans. Settlers have important needs for credit, such as lumber and building materials, horses, dynamite for clearing land, and farming equipment. They need credit for groceries, feed, and other supplies, when they have little income (Table XXXV). The majority of these loans were obtained on notes and chattel mortgages, but some were obtained on real estate mortgages. No federal land bank loans are included in this tabulation. The average interest rate for short-term loans was 7.7 per cent; for real estate mortgages, 6.5 per cent.

TABLE XXXV

PURPOSES OF 633 LOANS OBTAINED BY SETTLERS IN MINNESOTA AND MICHIGAN, SUBSEQUENT TO FIRST PURCHASE OF LAND

Purpose of loans	Loans	Average interest rate,* per cent
Buy stock	157	7.6
Buy more land	46	6.4
Pay off land debt	205	6.7
Building	103	6.5
Living expenses	38	8.4
Feed	27	8.1
Clearing	17	8.1
Machinery	10	6.6
Miscellaneous	37	7.6
All sources	633	7.2†

* Not including rates on federal farm loans.

† Real estate mortgages, 6.5 per cent; short-time loans, 7.7 per cent.

Interest rates on loans were higher in northern Minnesota than in northern Michigan, the average for Minnesota alone being 8.6 per cent on note-secured loans and 9.3 per cent on chattel mortgage loans, or 8.7 per cent on both combined. On note-secured loans from banks alone, the average rate in Minnesota alone was 8.9 per cent, ranging from 8.2 per cent in one area to 9.7 per cent in another. The average rate on all short-term loans in the cut-over regions of the Upper Peninsula of Michigan and of Wisconsin were about 7.6 per cent, and in the cut-over region of Lower Michigan they were still lower.

Several land companies in 1920 and 1921 were providing considerable short-term credit for settlers on the basis of either chattel mortgages or clauses in contracts that allow them to add the amount of such loans to the purchase price of the land. The land company most liberal in this respect was advancing funds for buildings, livestock, machinery, dynamite, and living expenses for the settlers while they were clearing the land, and machine and horse labor at land clearing. The settlers on this project had increased their debts an average of $874 during the first two years after settlement, but they had cleared over 10 acres of land and added $900 to their building, livestock, and equipment inventory.[18]

INTERMEDIATE CREDIT

Intermediate credit is commonly defined as credit for periods of from six months to three years. As notes commonly run for more than six months and real estate mortgages are sometimes made for less than three years, there is some overlapping of sources of short-term, intermediate, and long-term credit. Direct sources of intermediate credit to the farmer are individuals, savings banks, trust companies, country banks, co-operative credit associations, agricultural credit corporations, cattle loan companies, trade and mercantile institutions, and co-operative marketing associations.[19] The secondary sources through which the primary sources rediscount are individuals who buy such paper from banks for investments, intermediate credit banks, and federal reserve banks.[20] The intermediate credit banks may in turn sell their debentures to federal reserve banks, insurance companies, various kinds of banks and trust companies, and individuals.

[18] Settlement and Colonization in the Great Lakes States, by J. D. Black and L. C. Gray, U.S. Dept. Agr. Bull. 1295, p. 73. 1925.

[19] Farmers get a considerable amount of intermediate credit from the country banks through the process of renewing their notes. The principal sources of intermediate credit in Minnesota are trade and mercantile companies and banks.

[20] The agricultural credit act of 1923 amended the federal reserve act to permit the federal reserve bank to rediscount farm paper from member banks for a period up to nine months.

Until 1923 there were no special governmental institutions organized to supply the farm credit needs of the intermediate type. After the break in prices in 1920 and 1921, many farmers found it impossible to pay their debts to the banks, and with declining deposits the banks, in turn, were hard pressed. Many economists, farm leaders, and bankers were of the opinion that banks organized primarily to supply industry and trade were not in position to supply farmers' intermediate credit needs. It was said that commercial banks must keep their funds invested in short-term paper in order to be able to repay depositors on short notice. On June 7, 1921, Congress provided for a Joint Commission of Agricultural Inquiry. In its report this commission said: "The Commission believes that the difficulties of agriculture are in part due to the credit restrictions and limitations of the past 18 months, and in part are due to the fact that the banking machinery of the country is not adequately adapted to the farmers' requirements."[21] In 1923 Congress provided for twelve intermediate credit banks. One such bank serves each federal land bank district and is located in the same city as the district federal land bank. The bank serving this district is located in St. Paul and has the same officers as the land bank except that a special officer is manager. The position of the intermediate credit banks in financing agriculture has been said to be similar to that of federal reserve banks in financing commercial and industrial enterprises. Such a statement can be made because the farmers of the country never really understood that federal reserve banks were established to help them as well as trade and industry. They did not appreciate the federal reserve banks because most rural banks did not and do not now belong to the system.

A farmer can not borrow directly from intermediate credit banks. He must borrow through co-operative marketing associations, agricultural credit corporations, livestock loan associations, or local banks. If loans were to be made direct to farmers, cumbersome machinery would be needed. As it is, the farmer must learn to help himself through his own co-operative organizations or through agricultural credit corporations if he is not well served by his local bank. The direct loans to farmers' co-operative associations are made only on the basis of agricultural commodities, and the loans are secured by warehouse receipts. The federal farm loan board has approved the following commodities, when properly stored, as acceptable for security on warehouse receipts: Grain, cotton, wool, tobacco, beans, rice, alfalfa, red-top and clover seed, hay, nuts, dried fruits, maple syrup, honey, broom corn, and canned fruits and vegetables.[22] The board may add other commodities to the list when it has determined whether they can be stored so that warehouse receipts based on them will make good collateral. Potatoes, an important product in Minnesota, handled to some extent by co-operatives, do not appear in the list of approved commodities.

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[21] Report of the Joint Commission of Agricultural Inquiry, Part II, p. 7.

Volume of Business of Intermediate Credit Banks

The amount of direct loans to co-operative marketing associations and the commodities loaned upon by the twelve intermediate credit banks at the close of business December 31, 1927, are given in Appendix Table 2. Co-operative marketing associations in the St. Paul district, which serve Minnesota, North Dakota, Wisconsin, and Michigan, were using this source of credit to the extent of $847,848. In the Springfield, Omaha, and Spokane intermediate credit districts, co-operatives were borrowing still less. Districts in which tobacco, cotton, and raisins were marketed co-operatively had the largest borrowers. Co-operatives in the Berkeley district borrowed nearly 6 million dollars on raisins alone.

The most valuable field of service for the intermediate credit banks has been in financing co-operative marketing organizations. On December 31, 1927, the direct loans to co-operative marketing associations in the United States totaled $31,990,597. The service to co-operatives has been particularly valuable in the South and West. On December 31, 1927, loans to co-operatives in the intermediate credit districts surrounding New Orleans, Berkeley, and Wichita ranged from 4 to 6 million dollars. They were about half as large in the Baltimore and Columbia districts; between one and 2 millions in the Louisville, Houston, and St. Louis districts; and less than one million in the St. Paul, Springfield, Spokane, and Omaha districts.

On April 7, 1928, the Intermediate Credit Bank of St. Paul rediscounted notes for banks, agricultural credit corporations, and livestock loan companies to the extent of $7,550,013 (Table XXXVI). On December 31, 1925, these three institutions were rediscounting only $3,040,847, and on December 31, 1926, $4,440,464. This represents a rapid expansion of business. This increased demand for loans has come largely through the agricultural credit corporations and almost none of it through the banks. A partial explanation for this is the acute psychological conditions surrounding solvent banks. In communities where one or more banks have failed, the solvent banks have frequently deemed it necessary to invest their surplus funds in paper having a daily market in order to protect themselves against possible "withdrawal runs."

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[22] Federal Farm Loan Board, Circular 15, p. 18. 1925.

The Intermediate Credit Bank of St. Paul has financed the North Dakota Wheat Growers' Association and the Northern Wisconsin Co-operative Tobacco Pool for the crop seasons of 1923 to 1927. It has financed the Door County Fruit Growers' Union of Sturgeon Bay, Wisconsin, during the crop seasons from 1924 to 1927 and expects to finance the 1928 crop. It also has financed the North Dakota Co-operative Wool Marketing Association on the 1925, 1926, and 1927 clip. Intermediate credit has not been available to potato co-operatives. Co-operative butter marketing organizations have not needed credit of the intermediate type. There is a possibility of cheese being favorably passed upon as a suitable product for warehouse receipt loans, and if it is, the Wisconsin cheese producers will undoubtedly make some use of such credit.

TABLE XXXVI

REDISCOUNTS AND DIRECT LOANS OF INTERMEDIATE CREDIT BANKS AT CLOSE OF BUSINESS, APRIL 7, 1928*

District	Rediscounts†			Direct loans
	State banks	Agricultural credit corporations	Livestock loan companies	Co-operative marketing associations
Springfield	......	$ 667,927	....	....
Baltimore	$203,512	1,907,733	....	$ 1,696,301
Columbia	38,787	6,165,573	....	890,000
Louisville	41,613	211,646	....	1,395,768
New Orleans	......	5,731,578	$ 145,318	4,090,004
St. Louis	32,434	557,118	672,928	767,451
St. Paul	52,165	7,497,848	....	579,172
Omaha	......	....	5,576,941	344,041
Wichita	42,506	217,833	501,178	4,264,659
Houston	1,268	673,620	6,856,196	1,500,000
Berkeley	......	3,174,965	5,545,297	6,864,476
Spokane	......	2,816,241	2,573,141	371,604
Total	$412,286	$29,604,084	$21,870,999	$22,763,476

* Data from monthly statement of Federal Farm Loan Board.

† National banks were rediscounting $7,900 with the Springfield bank. Savings banks and Trust companies, Houston, $20,000.

Various reasons have been advanced as to why greater use has not been made of the intermediate credit banks. One reason is that the individual farmer has found it difficult to establish relations with his district bank, as he can not borrow directly. Local banks, unless hard pressed, are inclined not to rediscount in order to extend the volume of their loans. Further, until March, 1927, banks were not permitted to charge an interest rate of more than 1½ per cent above the intermediate rediscount rate on rediscounted paper. In March, 1927, the margin allowed was increased to 2½ per cent. There is no limitation as to the margin taken by the local bank if its paper is rediscounted with the federal reserve banks and the rediscount rate from the latter has been below that of the intermediate credit banks. Furthermore, the law limits the volume of rediscounts that a bank may have with intermediate credit banks to 2½ times its capital and surplus, while there is no such legal limit in rediscounting either with federal reserve banks or with city correspondent banks.

On January 1, 1927, there were 51 agricultural credit corporations in North Dakota, 7 in Wisconsin, and 18 in Minnesota. Two new credit corporations were organized in Minnesota during the last half of 1926 and three were discontinued. The location of the corporations in Minnesota on April 1, 1926, is shown in Figure 9. Following is a list:

Agricultural Credit Corporations—Minnesota

Farmers Credit Company, Claremont, Minn.
Otter Tail Loan & Investment Company, Fergus Falls, Minn.
Farmers Credit Company, Goodridge, Minn.
Greenbush Credit Company, Greenbush, Minn.
National Credit Company, Herman, Minn.
Farmers Credit Company, Kennedy, Minn.
Lake Park Cattle Loan Company, Lake Park, Minn.
Bankers Dairy Credit Corporation, Minneapolis, Minn.
Montevideo Agricultural Credit Company, Montevideo, Minn.
Farmers Credit Company, Oslo, Minn.
Farmers Credit Company, Redwood Falls, Minn.
Northwestern Agricultural Credit Corporation, St. Cloud, Minn.
Farmers Credit Company, Stephen, Minn.
Farmers Credit Company, Tyler, Minn.
Walnut Grove Credit Company, Walnut Grove, Minn.
Mahnomen County Cattle & Credit Company, Waubun, Minn.
Faribault County Credit Company, Wells, Minn.
Northwest Farmers Credit Association, Pipestone, Minn.

Indications are that the agricultural credit corporations in Minnesota will form the chief connecting link between the farmer and the Intermediate Credit Bank of St. Paul. These institutions are organized under the state general incorporation law.[23] Shortly after Congress provided for the intermediate credit bank system a number of banks in Minnesota organized small agricultural credit corporations with a minimum capital of $10,000. Following good banking standards, the management of the bank in St. Paul refused to rediscount all poorly secured paper. Its acceptance of well secured paper has given a much needed service to many banks. Many of these early corporations had either liquidated or were inactive by the beginning of 1927. As, theoretically, the intermediate credit banks are not to compete with local banks, the advisability of establishing a large number of small organizations may be questioned. A few large organizations are now reaching out over a large territory for loans, notably those in Minneapolis and Pipestone. There will probably soon be enough large agricultural credit corporations that their service in connecting the individual borrower with the Intermedite Credit Bank of St. Paul will be available to any farmer in Minnesota. A mere statement of the problem is sufficient to show that there are many unsolved problems in connection with the operation of such contact institutions.

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[23] The Minnesota legislature passed a special incorporation law intended for them during 1923-24 session, but because of restrictive features on loans, it has not been used.

The following extracts from letters indicate some of the services that may be rendered by the intermediate credit bank, through agricultural credit corporations:

From Mahnomen County Cattle Credit Company, March 30, 1926—

> "Most of the money we are loaning through our Association is for milk cows, steers, sheep, and hogs. We have found the Federal Intermediate Credit Bank of St. Paul very liberal on loans that are used to buy livestock.
>
> "Last year we shipped in two or three carloads of cows and steers together with two carloads of sheep. These proved to be very profitable to the farmers. We are planning on shipping in some more steers this spring, as last year the farmers made on the average $30 per head."

From the Lake Park Cattle Loan Company, March 31, 1926—

> "In reference to the method of operation of the Lake Park Cattle Loan Company, I wish to say that it is organized primarily for the purpose of lending money to farmers to carry on their farming operations by rediscounting such notes as it may become possessed of with the Federal Intermediate Credit Bank of St. Paul. These loans are proving very popular in this locality, as they provide the farmer with a reasonable amount of capital on easy terms. The rate of interest after April 1 will be 6½ per cent to the borrower, with loans made for from 9 months to a year with the privilege of renewal."

From Farmers Credit Company of Oslo, April 2, 1926—

> "Your favor of March 27 to the Farmers Credit Co. is received. . . . . The principal aim of our association is to make short-term loans and in that way be able to liquidate bank indebtedness. In this way it has worked out fine."

Agricultural credit corporations will probably increase in importance, but the system is too young for any prediction as to its future development. Livestock loan companies are finding intermediate credit banks a helpful source of credit for livestock production, as credit is needed for a considerable time. State and national banks are rediscounting in only a limited way. As agricultural credit corporations become more generally available, as cattle loan companies are organized, and as cooperative marketing associations become more efficient in grading, processing, and warehousing, the importance of the specialized intermediate credit agencies will probably increase.

THE PROBLEM OF THE LOCAL BANK

By far the most important part of our whole agricultural credit system is the commercial bank. As an agency for supplying credit and other needs of agriculturists, it has been rapidly expanding in importance. The increase in banking resources in Minnesota from 1900 to 1925 was 735 per cent when expressed in current dollars, and 328 per cent if expressed in dollars of 1913. Per capita bank deposits have increased greatly in every county in Minnesota (Fig. 14). The banking power increased relatively more rapidly in the middle west than in other sections of the country from 1900 to 1924 (Table XXXVIII). The eastern states lost 12 per cent in relative banking

BANK DEPOSITS PER CAPITA IN 1912 AND IN 1920

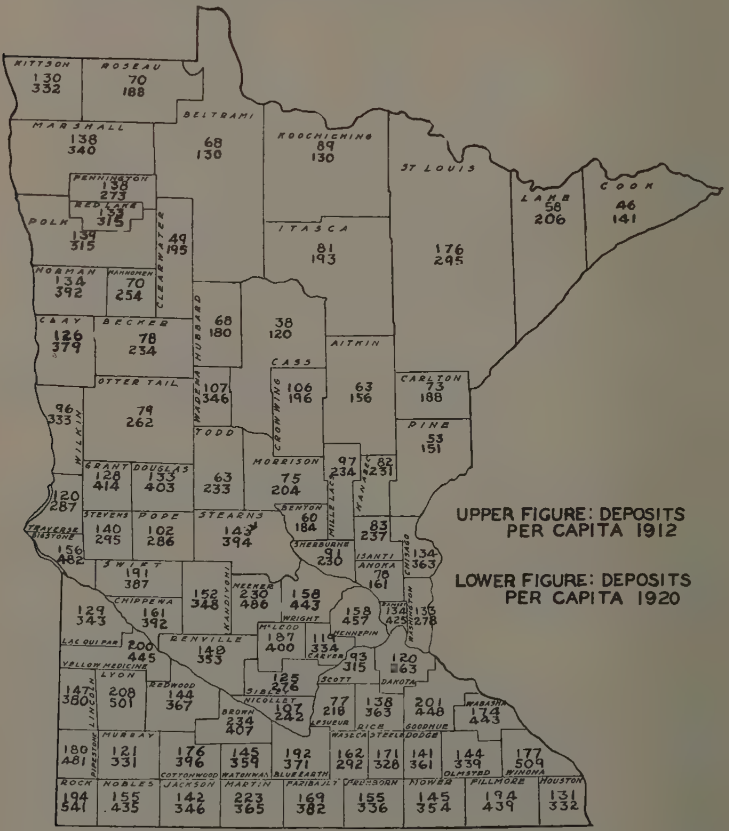

Fig. 14. Bank deposits per capita increased in every county in Minnesota between 1912 and 1920.

power during the first quarter of the nineteenth century, and the Middle West gained 16 per cent.

TABLE XXXVII

Growth of Bank Resources in Minnesota from 1900 to 1925

Date	Bank resources, millions*	Index number, wholesale prices†	Index number, dollars of 1913
June 30, 1900	$ 141.3	82.0	172.3
June 30, 1925	1,179.9	159.0	737.8

* Report of comptroller of currency, 1925, p. 94.

† All-commodity index number, U. S. Bureau of Labor.

The rapid growth of the banking habit in the United States in the last century is partly responsible for the growth of banks. The custom of using checks instead of cash in the settlement of money obligations is now widespread. The usual estimates are that at least 80 per cent of all payments are made by check. Checks are thus more important as a circulating medium in the United States than gold, silver, or currency. This change has enhanced the importance of bank deposits and of bank credit in the economy of the nation, and has made the regulation and supervision of the banking system a matter of greater importance and consequence to the welfare of the people.

TABLE XXXVIII

Change in Geographical Distribution of Bank Resources of the United States from 1900 to 1924

	Percentage of resources of all banks*		Percentage of change
	1900	1924	
East	66	54	—12
South	4	8	4
Middle West	8	24	16
Pacific Coast	4	7	3

* U.S. Dept. Agr. Yearbook, 1924, p. 194.

Banks Have Not Stood the Test

Yet in spite of this growth and great importance, the local banks have not stood the test in the financial upheaval through which we have just passed. Since 1919, 291 state banks and 65 national banks have failed, as compared with only 67 state banks and 6 national banks in the twenty-five years between 1894 and 1919 (Table XXXIX). Soon after the depression began, in June, 1920, state banks that had been borrowing heavily during prosperity began to fail. One bank was closed in 1920, but was reopened in about a month. The next year, 19 banks were closed, but 13 were later reopened. In 1922, only 15 banks were closed, and 8 reopened. Many people thought the worst was over; but then came 1923, with 43 banks closing and only 16 reopening later; then 1924 with 46 closing and only 14 reopening; 1925 with 36 closing and 3 reopening; 1926 with 78 closing and 4 reopening; and 1927 with 53 closing.

TABLE XXXIX

BANK FAILURES IN MINNESOTA, 1894–1927*

Year ended	State banks, savings banks, and trust companies		National banks	
	No. of failures	No. of banks	No. of banks	No. of failures
Aug. 31				
1894	2	216	79	
1895	5	232	79	
1896	6	218	76	
1897	7	206	71	3
1898		204	70	
1899		236	69	
June 30				
1900	2	252	76	
1901	2	275	92	
1902		307	117	
1903		350	171	
1904	13	386	213	
1905	3	456	224	1
1906	1	486	237	
1907	2	602	245	
1908	1	639	262	
1909	1	641	268	
1910		645	270	
1911		725	272	
1912	4	759	272	
1913		803	271	
1914	1	835	273	1
1915		925	277	
1916	1	1,014	281	
1917		1,105	287	
Dec. 31				
1918	2	1,148	294	1
1919	14	1,148	305	
1920	1	1,184	331	
1921	19	1,195	341†	
1922	15	1,175	330	
1923	43	1,159	344	3
1924	46	1,088	334	8
1925	36	1,057	318	11
1926	78	956	287	30
1927	53	882	285	13
Total	358			71

* National bank data to 1921, from report of comptroller of currency for 1920. Remaining data from annual reports of the comptroller. State bank failures up to 1918 from report of the comptroller of the currency for 1920 and from 1918 to 1927 from data furnished by the State Banking Department.

† As of September 6, 1921.

While this large number of failures is a result of the depression, nevertheless it shows weaknesses in the system. The banking system must meet the needs of depression as well as of prosperity. When from 46 to 78 state banks in one state fail in one year, the evidence of weaknesses in the groundwork of the system is conclusive. It is significant that the failures did not assume large proportions until four years after the depression, when ample credit was available for liquidating good but slow loans.

That Minnesota has been in the same plight as other states in the Northwest is shown by Table XL. For the seven-year period ending June 30, 1926, 316 banks failed in North Dakota, 239 in South Dakota, 183 in Montana, 34 in Wisconsin, and 212 in Iowa. In all states except Wisconsin, the percentage of state banks failing has been considerably higher than that of national banks. Wisconsin probably had, prior to 1920, more effective bank control laws than had many neighboring states. So far as banking laws and regulations have anything to do with bank failures, it would be the rules and regulations effective in the years just prior to 1920 that would have any bearing on failures following 1920. The statement that Wisconsin's rules and regulations were, prior to 1920, probably superior to those of the other states would require considerable investigation in order that one could be sure of his basic facts. The statement, however, is suggested by the fact that Wisconsin banking laws show that at least as early as 1915 the banking department strictly controlled the establishment of new banks.

The mere fact that a majority of banks in the chief agricultural states did not fail is evidence that it is possible to have such a banking system that an abnormal number of failures need not occur during severe depressions.

TABLE XL

BANK CLOSURES IN NORTHWEST STATES, 1920-26*

Year June 30	North Dakota		South Dakota		Montana		Wisconsin		Iowa		
	State	Nat'l	State	Nat'l	State	Nat'l	State	Nat'l	State	Nat'l	Private
1920	2	0	1	0	0	0	0	0	0	0	2
1921	51	3	1	1	10	3	0	0	2	2	4
1922	12	2	5	0	~~11~~	7	1	0	6	0	0
1923	19	3	7	5	29	12	3	1	3	2	3
1924	127	20	117	7	64	23	11	2	17	2	8
1925	31	6	31	8	5	7	6	2	52	7	9
1926	36	4	49	7	5	7	8	0	63	16	13
Total	278	38	211	28	124	59	29	5	143	30	39
Percentage closed†	38.9	21.0	37.7	20.6	48.1	20.6	3.6	3.3	36.7	8.3	66.1

* Report of comptroller of the currency, 1920-26.

† Based on number of banks in 1920, as shown by comptroller's report.

Why Banks Have Failed

The first approach to the reasons for bank failures is to examine the reasons given by the State Banking Department for closing the banks. Associated with frozen assets as causes of particular closures, were mismanagement, depleted reserves, criminal irregularities, worthless paper, and too much real estate; with depleted reserves were associated mismanagement, insufficient business, too large loans, and criminal irregularities; with excess loans were associated depleted reserves and too many second mortgages. These causes might readily be reduced to two—criminal irregularities and mismanagement. The first is not important. Frozen assets, depleted reserves, and excess loans appear most frequently as evidence of mismanagement.

As 15 of the 34 banks with depleted reserves re-opened, it appears that greater effort on the part of the officers of some of the banks in attempting to increase reserves by rediscounting would have kept these banks from being closed. The three banks closed because of excess loans all reopened.

Many of the banks that have failed since 1920 are still in the process of liquidation. The policy of the liquidation department is not to rush the sale of assets where there is a fair possibility of saving the depositors' money by waiting. The liquidation department deserves credit for keeping the costs of liquidation low. A man is left in charge of the closed bank only as long as he is producing economical results in the way of collections. Slow items are left to be collected by local agencies.

TABLE XLI

REASONS FOR STATE BANK CLOSURES, 1920 TO MARCH 18, 1926*

Cause of closure	No. closed	No. reopened
Criminal irregularities	7	0
"Frozen assets"	108	32
Depleted reserves	34	15
Excess loans	3	3
Too much accommodation paper and one-man bank	2	0
Worthless loans	2	0
Mismanagement and irregularities	4	1
Foreign paper	9	5
Too much real estate	1	0
Failure of correspondent bank	1	0
Run on account of North Dakota paper	1	0
Bankruptcy of president	1	0
Run on bank	2	0
Too many unsecured loans	1	0
Local quarrel	1	0
Total	177	56

* As given by A. W. Smith, examiner in charge of liquidation for the closures of Minnesota state banks.

A closer approach to the problem may be obtained from a letter sent out in September, 1924, by A. J. Veigel, state superintendent of banks. This letter undoubtedly sums up Mr. Veigel's conclusions as to the causes of bank failures and losses in other banks as he has found them in recent years. The principal causes he mentions are the following:

1. Excessive loans to officers. The department insists that this class of loans be reduced or eliminated. "What we need is bankers without other interests to take up their time and money."

2. Large and excessive loans. "If the note pouch contains small and diversified loans, the total losses are usually much smaller than if the average loan is large." The legal limit of loan to any one individual or firm is 15 per cent of the capital and actual surplus (Ch. 103, Sess. Laws, 1919). "If the surplus, as shown on the books, is impaired, only the unimpaired surplus can be used in figuring excessive loans."

3. Outside paper. This means loans to individuals or corporations not in the immediate territory of the bank. "Usually the bank's officials know little if anything about such paper, and are obliged to take the word of somebody else that it is good. Somebody often gets a commission on such paper and the rate of interest is usually high."

4. Exchange of paper, meaning the exchange of paper be ween banks with the written or oral agreement to take it back if not paid when due.

5. Other real estate and second mortgages. Banks should not hold large amounts of real estate, and "second mortgages should not be taken except to secure previous debts."

6. Too many banks. "Our department is encouraging and even urging certain banks to consolidate, where conditions warrant such action."

7. Too small minimum capital. "We believe that the minimum capital of banks, which is now $10,000 to $25,000, according to the size of the city, should be increased. That would add a margin of safety for depositors, to which they are entitled."

8. Too much borrowing.

9. "One man bank." This means a bank whose directors are mere "dummies" or "rubber stamps." "It is the duty of directors to know what is going on in a bank."

Failures Due to Too Small Banks and Too Many

It is common opinion that banks fail largely because they are small and their resources are inadequate. Of banks capitalized for $15,000 or under, 21.2 per cent failed during the period; of those capitalized for $35,000 and over, 21.9 per cent; and of those between $15,000 and $35,000, 21.7 per cent (Table XLII). There is no evidence that small capitalization is a cause of failure. The reason that more banks of the lesser capital stock fail is that there are more of them. The losses sustained by the failure of a large bank are usually several times those sustained by the failure of a small bank. Probably, however, people are more disturbed over the failure of ten banks of $10,000 capital each than by the failure of one bank of $100,000 capital. Capital stock is not a good measure of the size of a bank's business. But the fact that 346 banks out of 432 with capital stock of $12,000 or less safely weathered the storm of depression between 1920 and 1926, suggests that a small bank can be as safely managed as a large one.

TABLE XLII

NUMBER AND PERCENTAGE OF MINNESOTA BANKS CLOSED ON BASIS OF CAPITAL STOCKS FOR PERIOD 1920 TO END OF 1926*

Capital stock†	Banks	Closed‡	Closed
			per cent
$10,000	401	80	20.0
12,000	31	6	19.4
15,000	153	38	24.8
20,000	102	16	15.7
25,000	234	57	24.4
30,000	56	12	21.0
32,000	1		
35,000	6	1	16.7
40,000	19	2	10.5
50,000	79	17	21.5
60,000	8	3	37.5
75,000	7	2	42.9
100,000	23	2	8.7

* Savings banks and trust companies not included.

† As of June 20, 1920.

‡ Capital Trust Bank of St. Paul not included.

The total number of national and state banks, including trust companies and savings banks, per $1,000,000 deposit, for each county in 1920, with the percentage of closures in each county for the years 1920 to 1925, inclusive, is shown in Figure 15. In general, the more banks per $1,000,000 deposits, the larger the percentage of failures. The relationship is by no means close and there are many outstanding exceptions.[24] Too many banks is probably the largest single cause of bank failures. The argument against small banks is not so much on the score of their being small as that small banks may mean too many banks, too high unit costs of operation, too much competition for loans, and a general weakening of the whole banking system.

Failures Due to Agricultural Loans

There can be no doubt that the depression in agriculture following 1920 is the first cause of the epidemic of bank failures. If evidence is needed, it is given in the two maps in Figure 16, the upper showing the proportion of bank loans to agriculture, and the lower, the

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[24] The simple coefficient of correlation was 0.35 out of a possible 1.00.

NUMBER OF BANKS PER MILLION DOLLARS OF DEPOSITS AND PERCENTAGE OF BANKS FAILING BETWEEN 1920 AND DECEMBER 31, 1925

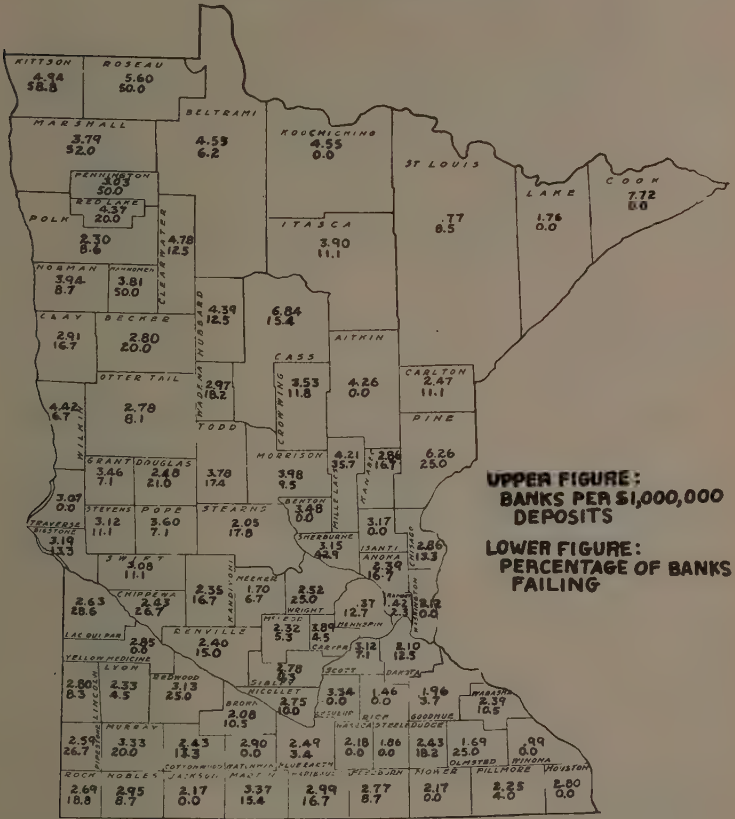

Fig. 15. In general, the more banks per million dollars deposits the larger the percentage of failures.

number of bank failures. Failures are most numerous where agricultural loans are high. Failures in Minnesota have been most numerous in relation to the population away from city centers, even after allowance is made for difference in size of banks. By types of farming, they have been most numerous where farming includes the most cash crops, the Red River Valley having suffered most and the dairy region least (Fig. 17).

The fundamental reason why more banks fail in the farming centers than in the industrial centers when a general depression strikes the

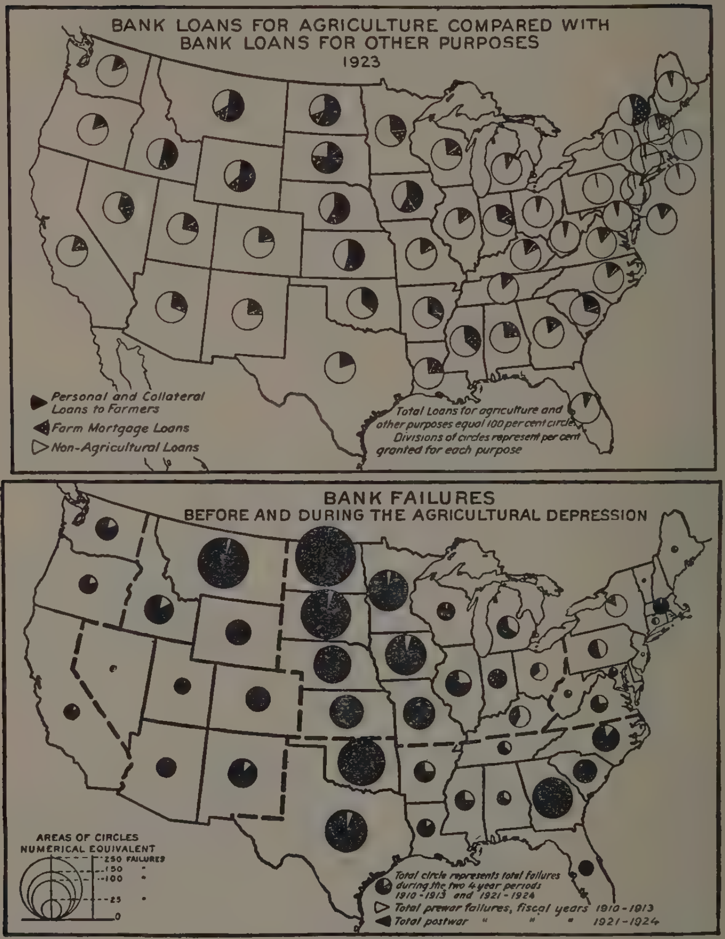
BANK LOANS FOR AGRICULTURE COMPARED WITH BANK LOANS FOR OTHER PURPOSES
1923
Personal and Collateral Loans to Farmers
Farm Mortgage Loans
Non-Agricultural Loans
Total Loans for agriculture and other purposes equal 100 per cent circle. Divisions of circles represent per cent granted for each purpose
BANK FAILURES
BEFORE AND DURING THE AGRICULTURAL DEPRESSION
AREAS OF CIRCLES
NUMERICAL EQUIVALENT
250 FAILURES
150
100
25
0
Total circle represents total failures during the two 4 year periods 1910-1913 and 1921-1924
Total prewar failures, fiscal years 1910-1913
Total postwar " " " 1921-1924

Fig. 16. Maps from U.S. Dept. Agr. Separate No. 1915. Farm Credit, by Nils A. Olsen.

Upper.—A department survey shows that bank loans for agricultural purposes in 1923 amounted to about 14 per cent of the total loans and discounts of all state and national banks. Farm mortgage loans amounted to 4.5 per cent and personal and collateral loans to 9.5 per cent of bank loans to farmers.

Lower.—Bank failures between June 30, 1920, and June 30, 1924, totaled 1,960, as compared with 202 during the four years 1910 to 1913. Most of these were in the farming sections of the country. While the depression in agriculture was a large factor in these failures, inadequate resources and inefficient banking methods were important contributing causes.

country is that agriculture can not adjust itself to a lower price level as quickly as can industry. When an industrial plant can not sell its products at a price sufficient to cover cost of operation, it is closed. This reduces production and keeps the price of the product from falling so far as it otherwise might. Part of the loss of shutting down is shared by the unemployed laborers. When the closed plant ceases to buy raw materials, the prices of raw materials decline rapidly and the producers on the farm and elsewhere find themselves sharing some of the loss. As the supply of manufactured goods declines and the price offered for them approaches the former level, the plants are opened again and laborers are hired at a wage much nearer the former wage level than would likely have been possible had the plant continued in operation.

LOCATION OF STATE BANK FAILURES, 1920 TO 1926, INCLUSIVE

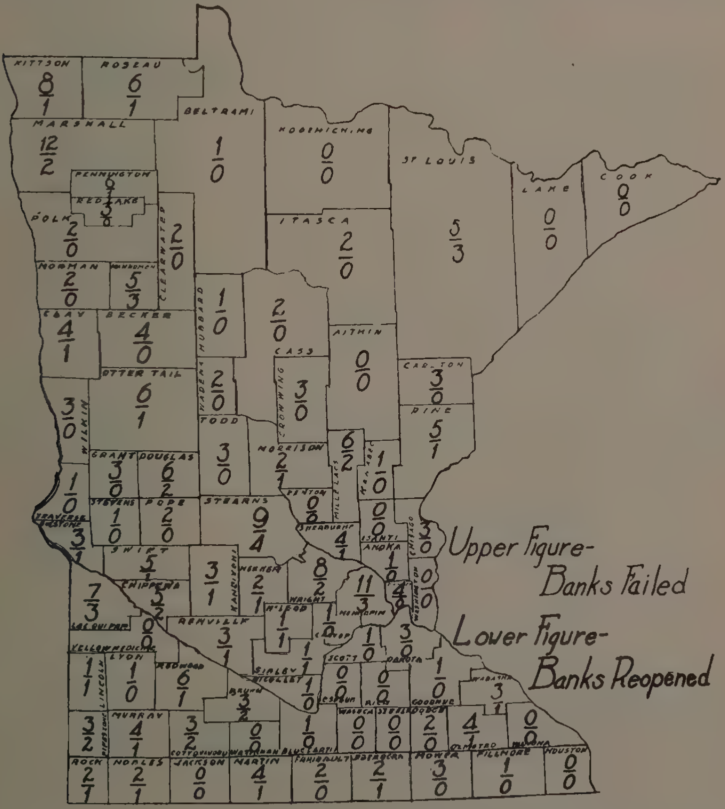

Fig. 17. Failures have been most numerous in relation to population away from the city counties even after allowance is made for the difference in size of banks.

The farmer, on the other hand, can not close down. He can not stop milking the cows, cultivating the corn, or cutting his grain and come back a few months later and start the farm factory going again. When prices broke in 1920, the farmers' crops were already planted with costly seed and labor and could not be harvested until months later. Moreover, farming is to a large extent a family business with three-quarters of the man labor performed by the owner and his family. If the farmer leaves the farm, he loses a home as well as a job. With a fall in prices, the hired help may be dismissed, but taxes and interest must be paid when due and the family must live. When prices decline sharply, the farmer often feels that more must be produced to meet the fixed annual expenses. Repairs are delayed, improvements are postponed, but men, women, and children work harder and longer in order to produce more at lower prices to maintain the necessary income.

Also, ownership of a farm is an individual matter and the risks of ownership are not scattered, as is usually the case with a corporation. It takes the major part of a man's lifetime to become a complete farm owner; hence most farmers are in debt. Much of the capital invested in farming is more or less fixed. A dairy cow does not reach her prime for five or six years and does well to pay for herself when eight years old. Tile drains and buildings require many years to pay for themselves. The cost of removing stumps and stones must be spread over many years. Because of this, the rate of turnover in agriculture is very slow compared with that in industry, hence agriculture adjusts itself much more slowly to deflation.

The effects of the foregoing are most clearly seen in a comparison of prices of farm products and other products from 1914 to 1926 with those of 1913, as in Figure 18. Beginning in June, 1920, all prices fell rapidly. But the wholesale price index for all commodities fell only from 231 to 170, while the index of farm prices fell as follows:

Date	Farm price level, per cent of 1913[25]
January, 1920	247
June, 1920	237
January, 1921	143
June, 1921	114

In May, 1920, the price of wheat was $3.00 a bushel. By the following December the price had declined to $1.68. In June, 1920, corn was selling at $2.00 and in December at 76 cents. As agriculture was unable to curtail its production to suit the new economic conditions, its products continued to fall in price while factory products soon began to recover. This reduced the purchasing power of farm products, as shown in the lower curve in Figure 18.

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[25] Bureau of Labor Statistics, Bulletin 367, p. 18.

However, the reason that so much of the agricultural bank paper of the period of depression is not liquid is not that price levels are so far out of line now as that the things the farmer sells are now so much cheaper than during the war and the two post-war years when he contracted his debts. On the basis of war incomes, many farmers bought machinery, buildings, land, automobiles, and better livestock on credit at high prices. It is difficult to pay interest and principal with farm commodities from 25 to 50 per cent below the level at which the debts were incurred. Farmers who did not go into debt at war prices have continued to progress financially. The farmer may greatly curtail his buying by getting along without many things he would like to have, but he can not avoid paying for the goods he bought at a war time price level of 200 to 270.

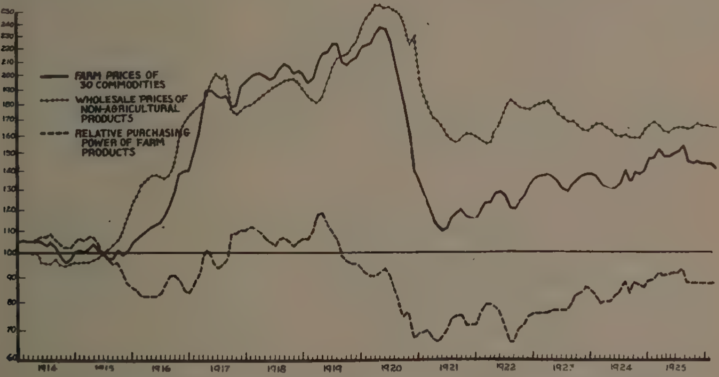

Fig. 18. Relationship of Wholesale Prices of Agricultural and Non-agricultural Products and Their Ratio from 1914 to 1926. Base Year, 1910-14

The great increase in taxes and railroad rates after 1920 added still further to the farmers' disadvantage. Taxes in Minnesota for 1921-22 were 246 per cent of what they were in 1913-14;[26] the average freight rates on 50 representative agricultural products in the United States were 159.8 per cent of the 1913 rate.[27] The rate on wheat from Tracy to New Ulm, Minnesota, on January 1, 1913, averaged 121.7 per cent of the 1913 rate. The rate on oats from McIntosh to Minneapolis, in 1923, was 144.2 per cent of the 1913 level.[28]

Failures Due to Bad Management

If banks are to be kept from failing in periods of depressed prices, they must be reasonably well managed. Neither poor management nor depression alone ordinarily will cause bank failure, but a combination of the two. A poorly managed bank will get along till a crisis comes and will then be wiped out.

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[26] U.S. Dept. Agr. Yearbook, 1922, p. 1002.
[27] U.S. Dept. Agr. Yearbook, 1922, p. 1011.
[28] U.S. Dept. Agr. Yearbook, 1922, p. 1014.

The bankers did their worst banking just at a time when their best was needed. Their experience had been such as to unfit them for handling the problems of 1919 and 1920. During the preceding 23 years of rising price levels for farm products, farm incomes had gradually increased. Rising incomes had resulted in an increased capitalization of farms. The result was that loans to farmers had generally been good. Country bankers had found by experience that the farmers' business was sound, and they competed for it actively. Excessive loans on real estate were usually well secured by the time the loan matured, because of rising land values. The increased demand for food following the opening of the World War, in August, 1914, caused prices of farm products to rise sharply. Bank deposits increased rapidly (Fig. 19). Farmers soon paid their current obligations to the banks and to the

CHANGES IN SAVINGS ACCOUNTS, TIME CERTIFICATES, AND CHECKING ACCOUNTS FOR MINNESOTA STATE BANKS

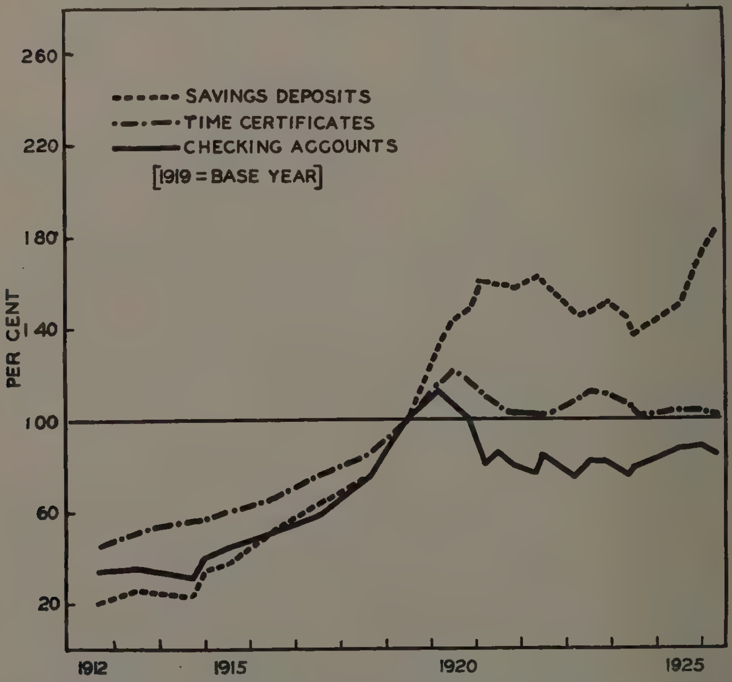

Fig. 19. Checking accounts increased 156 per cent, savings deposits 192 per cent, and time deposits 95 per cent from June 23, 1915, to February 28, 1920. Checking accounts declined about 36 per cent in 1920. Savings accounts have continued considerably above the 1919 level while checking accounts at the end of 1925 were roughly on the 1918 level.

business men. Prosperity became rampant and business conditions changed. The rapidly growing deposits neutralized the seasonal fluctuations in demands for money and many bankers became more careless in extending credit. It was well known that many loans made would need to be renewed at maturity. Banks that had been persistent borrowers paid off their debts with the large supply of loanable funds that came to them. The new prosperity filled both bankers and their customers with a spirit of optimism. Bankers began to encourage borrowing by farmers and business men in order to employ their loanable funds. Because of profits from increased value of inventory between purchase and sale, customers responded readily to the easy credit opportunity. When the war ended, expansion halted for a time, as depression was generally expected. Soon, however, prices began rising again because of heavy purchases by Europe on money borrowed in the United States and the $25 per capita contributed in the United States to the Red Cross.

The banks further expanded their loans. People who had been saving during the war cashed their liberty bonds freely in order to spend the proceeds. Conservatism gave way to extravagance and speculation. Old standards of credit analysis and principles of lending were forgotten, and as the "economic spree" continued, loans were made with almost unbelievable liberality.

In order to obtain high interest rates and liberal discounts collectable on customers' notes, banks began to borrow larger and larger amounts as the period of expansion continued. Borrowings increased during the war period, especially in the period after the United States entered the war, but they increased more rapidly in 1919 and 1920 while the land boom was rampant (Table XLIII). Few bankers were concerned with the fact that the rapid inflation of values was largely caused by the great expansion of bank credit in the banking system, and the failure of the Federal Reserve Bank to raise the discount rate so that the government might float the Victory loan at a low rate of interest.

Finally, as the expenses of business overtook business profits, the expanding price level and the shrinking value of the dollar came to an abrupt end in June, 1920. Banks soon found that owing to falling incomes, farmers were unable to reduce the amount of their short-time current loans. At first it was generally expected that prices would soon recover, and the banks had to renew loans and did so rather willingly. This necessitated more borrowed money to maintain the reserves, which were declining rapidly owing to declining deposits. Bills payable and notes rediscounted for state banks increased over 11 million dollars after June, 1920, and did not reach their height until late in 1921 (Table

XLIII). The increase in borrowed money after June, 1920, was about seven times the total amount borrowed in 1915.

TABLE XLIII

MONEY BORROWED BY MINNESOTA STATE BANKS AT VARIOUS DATES BETWEEN 1910 AND 1927*

Date	Thousands
June 30, 1910	$ 486
June 7, 1911	1,177
June 14, 1912	790
August 9, 1913	1,110
June 30, 1914	1,208
June 23, 1915	1,713
June 30, 1916	2,006
July 25, 1917	3,489
June 29, 1918	6,977
June 30, 1919	4,199
December 31, 1919	8,117
June 30, 1920	17,044
October 6, 1920	24,177
November 15, 1920	27,461
February 21, 1921	28,241
June 30, 1921	28,194
October 6, 1921	28,504
December 31, 1921	27,815
June 30, 1922	20,658
June 30, 1923	13,608
June 30, 1924	9,897
June 30, 1925	4,586
December 31, 1925	3,975
March 15, 1926	3,338
June 30, 1926	4,337
November 13, 1926	4,390
December 31, 1926	4,072
December 31, 1927	2,839

* From Abstracts of the State Banking Department.

In attempting to maintain their reserves against declining deposits and slow liquidation, the banks raised the rate of interest on time deposits. Probably this was a mistaken policy, as it appears to have resulted only in withdrawal of small funds from banks that did not raise their rate of interest and their deposit in those that did. Bank expenses were increased when they should have been lowered. It is questionable whether a higher rate of interest induces an immediate increase in savings.

Too frequently credits to farmers and merchants were so excessive that the face of the loan was greater than the value of the security or any security that the debtors could offer on the basis of the new price level. The volume of losses from such loans need not be very large to cause a small bank to fail. Too many banks of all sizes had paid 20 per cent dividends in 1919 and 1920 instead of creating a large reserve for losses. Where the farmer could supply ample land security, hundreds of banks were saved by the farmer funding his current indebtedness into a long-time real estate loan. The Minnesota Rural Credit Bureau probably saved scores of banks by accepting several hundred marginal land loans during 1924. Loans made by the Minnesota Credit Bureau also gave the farmer an opportunity to save his farm and home by spreading the payment of his debt over several years with a low rate of interest.

COMMERCIAL STATE AND NATIONAL BANKS IN MINNESOTA

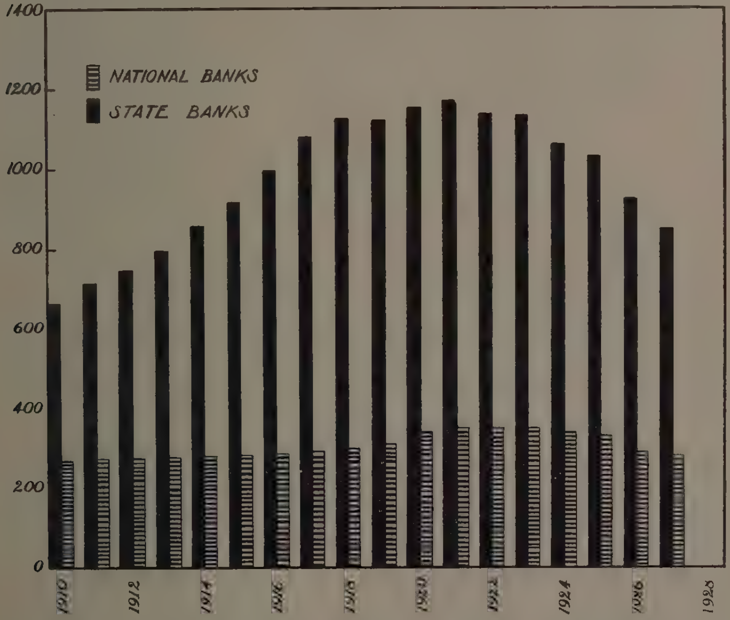

Fig. 20. Through consolidation and failures the number of state commercial banks and national banks in Minnesota at the end of 1927 has been reduced to the level of 1915.

The period of adjustment to the new price level was marked by political unrest, bankruptcy, bank failures, and reversion of land to former owners. The public knows little of the hundreds of owners of bank stock that have been compelled to pay assessments to put their banks on a solvent footing. Through consolidations and failures the number of banks in 1927 was reduced to that of 1915, as shown in Figure 20 and Table XXXIX. As a whole, the banks of Minnesota are now thought to be in better financial condition than at any time since 1920. Most banks are independent of outside capital.

"Frozen Assets"

Probably the term "frozen assets" has been too freely used as an explanation of bank failures. It is true that banks found themselves in too many instances with slow notes of farmers and merchants in their files. However, if there had been ample security behind these slow notes, they could have been rediscounted or the security sold and thus liquidated. It is doubtful if a well-secured note, even in the depths of depression, could not have found a market. But the so-called "frozen" notes found in the bank files were often entirely unsecured, often signed by individuals or corporations whose financial rating never warranted a credit extension as large as the face of the notes, and in many cases the secured notes were secured by property that had come to be worth less than the face of the note. Thus in many cases the notes were worthless or nearly so. That many of the "frozen credits" were worth less than their par value is shown by the fact that many banks failed long after credit became plentiful. As has been said on several occasions, the "frozen assets" have often proved to be "rotten" when they started to "thaw."

Banking Regulation as a Means of Improvement

In general, there are three lines of attack on the problem of improving country banking. One is to set up more overhead institutions to work with the banks and co-ordinate their activities. It seems that with the three types of federal banking institutions we can rest for a while and learn to make proper use of what we have. Another is to adopt research and educational programs for the purpose of improving local management. The possibilities of this have been barely scratched. The third is to develop a higher order of regulation of these activities. The third method everyone turns to first. And surely banking is a type of business that must submit to a large measure of public supervision and control.

In Minnesota, public interests have been safeguarded by an efficient Department of Banking; but the powers of the department have been limited in some important respects. The general philosophy has been the same as in other central western states, namely, that the public would be best served if individuals were allowed to engage freely in the banking business with as little supervision and control as possible. Under this system, many small independent banks have developed, the capital of which has been largely contributed by the community in which the bank is located. The officers and directors of each bank usually are local men interested in using the funds of the bank to develop local industries. Prior to 1920, charters were granted without much restraint. People in Minnesota have generally objected to control of local banks by outside capital. Branch banking never made any substantial progress and was prohibited by law in 1923. (Chapter 170, Session Laws 1923.) The capital requirements established by law have been so low that a bank could be established at every hamlet or country trading center.

Prior to 1919 the number of banks that might be established at one point to compete for business was unlimited, with the result that the number of small banks increased rapidly. It is not unusual to find two or more banks in small towns where there should be only one. The cost of credit has been needlessly high—the entire banking buisness of most communities could have been easily performed with one overhead charge instead of two or more. Surely two banks of $50,000 capital each could be run more cheaply and serve the community better than four banks of $25,000 capital each.

The advice given by Kelsey S. Chase, superintendent of banks in 1912, is to the point. He says, "There have been thirty-five banks chartered during the past six months, almost all of which were organized with a capital of $10,000. The prosperity of Minnesota and of any community within the state is not enhanced by a large number of banks, but its prosperity does depend in part upon the strength of its existing banks. Almost any three or five individuals can organize and operate a bank for a time, and no one can lawfully prevent them, even tho the incorporators might be absolutely incompetent and financially irresponsible. Often the seed which later develops into a second bank in a community where only one bank is needed is sown through local jealousies and factional quarrels. Irresponsible parties who have been denied loans by the existing bank are often the most aggressive agitators for a second bank."[29]

Prior to 1910, banks and other financial institutions in Minnesota were under the jurisdiction of the public examiner. Private banks were not under state supervision until 1907. The laws of 1907 compelled private banking institutions to incorporate as banks or discontinue business, so there were no private banks in operation by November 1, 1909.[30] The establishment of the Department of Banking, in 1909, to enforce all banking laws was a decided step forward. While the legislature has always been friendly to the requests of the banking department for increased funds, the work required of the department has grown so rapidly that appropriations have not been sufficient to meet the increased demands. Salary limitations have greatly hampered the department. After a man is well trained to do bank examination work, he ordinarily has little difficulty in securing a $5,000 position with a private enterprise. This is more than the upper limit established by law to be paid to the superintendent of banks.

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[29] Third annual report, Dept. of Banking, p. XXIX.

[30] Report, Dept. of Banking, 1910, p. IV.

The work of the superintendent of banks[31] under the law is to exercise a constant supervision over the books and affairs of all state banks and other financial corporations and, through the examiners provided for, visit all state banks at least twice each year and investigate the character and value of their assets. He is required further to investigate the method of operation and conduct of such corporations and their system of accounting, and to ascertain whether such methods and systems are in accordance with the law and with sound banking principles. He may examine, or cause to be examined, on oath, any officer, agent, customer, or depositor of any bank on matters touching the business thereof, and compel access to such books, accounts, documents, and property as he may desire to inspect. No examiner may examine any bank in which he is interested directly or indirectly.

Changes in Banking Laws

During the last few years, marked progress has been made in remedying elements of weakness in the law relating to bank regulation and administration. The following are the more outstanding changes made. The Minnesota State Bankers Association has almost without exception taken the lead in securing these reforms.

1. Perhaps the most important change has been that of granting to the State Securities Commission control over the granting of the initial charter for any kind of bank to be organized under the laws of the state. (Chapter 86, Session Laws, 1919.) Heretofore, weak, unnecessary, and poorly managed state banks have been organized by itinerant promotors who were interested only in collecting a liberal fee.[32] The law of 1919 enables the commission to deny a new charter where the need for additional banking facilities does not appear to exist, or where added competition would endanger the solvency of existing banks, or if the commission is not satisfied that the proposed bank will be safely managed. The practical working of this law is shown by the fact that 20 out of 42 applications for charters from July 1, 1923, to June 30, 1924, were denied.

2. Closely connected with the power granted the State Securities Commission to prevent, under certain conditions, an increase of state banks, is the permission given to existing banks to consolidate. With the written consent of the superintendent of banks, one bank may consolidate with another, but the transfer of assets and liabilities to another bank shall be without prejudice to the creditors of either. (General

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[31] Changed to commissioner of banks in 1925.

[32] Third annual report, Dept. of Banking, p. 7.

Statutes, 1913, 6373.) The consolidation of two banks may make one strong bank in place of two weak ones. The department has been encouraging such procedure. A. J. Veigel, superintendent of banks, says "Many cities and especially villages have too many banks. If a bank does not have enough business to pay reasonable salaries, dividends, charge off losses, and build up a surplus, it will probably not be a safe bank indefinitely. Our department is therefore encouraging and even urging certain banks to consolidate when the conditions warrant such action."[33]

3. The reorganization bill of 1925 changed the term of office of the superintendent of banks from two to six years. The effect of this change is to make the office less subject to political disturbances and influence. The activities of the Department of Banking in protecting the public interest must necessarily often interfere with the private activities of individuals having more or less political influence; hence the more nearly management can be divorced from political influence, the more efficient the management may become.

4. An important safeguard incorporated in the laws of 1925 deals with restrictions on loans to officers and directors. "No cashier or other officer or employee of a bank shall sell to such bank, directly or indirectly, any mortgage, bond, note, stock or other security whatsoever without the written approval of the board of directors filed in the office of the bank—and a copy sent to the State Superintendent of Banks." (Chapter 305, Session Laws 1925.)

"Every state bank shall be protected by good and sufficient sureties against unlawful acts of any of its officers or employees. The bonds must be satisfactory to the Superintendent of Banks." (Chapter 351, Session Laws 1925). This provision is an important recent safeguard adopted by law. Probably the law did not go far enough in this respect. A perusal of the annual reports of the banking department over a number of years conveys the impression that the banking department frequently felt that too many banks were managed like a private land company. The Royalton and Bowlus cases, described in the 1912 report of the banking department, show the extreme to which a bank may be looted by over-loaning to officers and companies in which the officers are interested. The day has passed when any banker may regard a bank as a private institution in the same sense as a real estate office.

5. The state banking department has for many years recommended to the legislature an increase in the minimum capital of banks, but the matter was not acted upon favorably until 1927. The 1927 legislature amended the former law regulating capital and surplus requirements as follows:

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[33] Letter to all state banks and trust companies, dated September 22, 1924.

Old law			New law		
Population of municipality	Minimum		Population of municipality	Minimum	
	Capital	Surplus		Capital	Surplus
			500 or less*	$10,000	$ 2,000
1,000 or less	$10,000	$2,000	500 to 1,000	20,000	4,000
1,000 to 1,500	15,000	3,000	1,000 to 2,500	25,000	5,000
1,500 to 2,000	20,000	4,000	2,500 to 100,000	40,000	8,000
2,000 or more	25,000	5,000	100,000 and over	50,000	10,000

* Left to discretion of securities commission, where there is no bank.

Under both the old law and the 1927 law there must be a paid-in surplus equal to not less than one-fifth of the capital stock. The new requirements apply only to banks hereafter organized, so if the present banks, as seems likely, constitute the bulk of the banks for a considerable period, the gains to depositors through a greater margin of safety are deferred to the future. A qualification should be noted—the 1927 legislature amended the banking laws so that no state bank or trust company shall accept deposits in a sum exceeding 25 times the amount of its capital and surplus. The increased capital requirements should tend to reduce the demand for new banks. Wyoming, Idaho, and Utah recently increased the required minimum initial capitalization of new banks to $25,000. In fact, the minimum is now $25,000 in most states.[34] Minnesota's minimum requirement appears to be rather conservative.

With the advent of improved roads and the general use of motor vehicles, there is less need for a small bank at every cross-road. No doubt people would be willing to travel a little farther for banking services if it would bring greater security for their deposits and help to insure a continuous loaning service instead of the recent disreputable situation, as a result of which in some communities there is practically no adequate banking service. Banks with larger capital and surplus would also have an advantage in being able to take care of the needs of the larger borrowers in the community, as the state law limits the size of loan to any one individual or corporation to 15 per cent of the capital and surplus of the bank. The considerable decrease in the value of a dollar from 1913 to 1926 makes the nominal increase in capital and surplus larger than the real increase in terms of purchasing power.

Further Changes Proposed

It is believed that the following further changes would assist still more in preventing epidemics of bank failures such as the recent one.

1. The appropriations for carrying on the work of the banking department ought to be increased and the salaries for the super-

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[34] Frank W. Simonds, Deputy Manager, A. B. A., *American Bankers Association Journal*, p. 327. November, 1925.

intendent and experienced examiners should be increased sufficiently to enable the department to compete successfully with private business for trained and experienced men. Chapter 136, General Laws 1919, provides that certain fees are to be charged for the examination of state banks, savings banks, trust companies, and building and loan associations, such fees to be paid into the state treasury and credited to the general revenue fund of the state. The fees earned by the department under this law during the fiscal years 1923 and 1924 amounted to $156,805.[35] The total expenses of the department for the two years were $269,657. Deducting the fees earned, the amount paid by the state for the two years is $112,852—an average of $56,426 a year. The small additional appropriation required to obtain and retain a competent personnel would be good economy for the people of the state.[36]

2. Another change in the law thought to be desirable is to reduce the number of mandatory examinations from two to one, because more time would be available for optional examinations where these are most needed. Many banks are run so conservatively that more than one examination a year seems to be useless.

3. Some plan should be evolved for giving the banking department control over the qualifications of local bank officers. At present no such control exists after a bank is once established. The basis of such control might be a licensing system by means of which minimum standards could be set up and enforced, such as are enforced for druggists. Through a licensing system the managers of banks might be required to have a knowledge of banking laws, to know something about price levels and business cycles, banking and investment principles, and to have had a reasonable amount of banking experience.

4. Greater protection should be provided savings depositors in commercial banks. It is proposed that the assets in which savings deposits are invested should be segregated and that it be unlawful to pledge any such assets as security for borrowed money. It is believed that savings depositors, more than checking depositors, suffer deprivation from bank losses. Furthermore, a bank usually borrows in order to make loans to customers having checking accounts. A checking account usually represents but a small part of the assets of any individual, and a partial loss of such accounts seldom results in actual personal deprivation. It seems appropriate to segregate the investments made with time deposit funds, and to make such securities not subject for any liability of the bank other than that to its time depositors.

5. County clearing-house associations should be established. The clearing-house idea is a part of the program of the clearing-house sec-

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[35] Department of Banking, Thirteenth Ann. Rept., p. 10.

[36] The 1927 legislature allowed an increase of $8,500 to the banking department.

tion of the American Bankers' Association, by whom it has been advocated for several years.[37] The clearing-house movement began in Chicago about 1905, after the Walsh bank failures, and has since spread to 32 cities and to a few country communities. The plan consists simply of a voluntary examination by an examiner employed by the association, who concentrates his attention on a few banks and whose reports serve as the basis of a credit bureau for improving banking conditions in the territory of the association. In organizing such an association, the banks of one county or of several counties combine for mutual protection, and agree upon certain banking standards. These standards should soon become the basis of increased public confidence.

A managing committee is selected and an examiner employed. The duties of the examiner are to make periodic thoro examinations of each bank in the association. All assets of the bank are examined, all notes and other assets and securities are carefully checked, and intra-bank borrowings detected. After such examination, the actual position of each bank is determinable. A complete report is made, which would furnish a basis of appraisal of the bank's ability to pay its depositors. The report should be frank and open and presented in person to the directors of each bank. Under the clearing-house system, no excuse exists for serious losses, and the public would be protected to the fullest extent.

Unless bankers can be held responsible for the banks that fail, there is no valid argument against the justice of government guaranty of bank deposits. When the federal government, the state, or a county deposits money in a bank, it usually requires a bond from the bank guaranteeing the safety of the deposit. The individual has as much right to be insured as has the government. State guaranty laws have generally been unsuccessful because insurance was attempted without respect to the risk and also because of political control. There are insurance companies that will insure bank deposits but not without selecting the risks to be insured.

The depositors have a right to some basis of discrimination between banks. Under the clearing-house system, the banks themselves provide such a system. Banks not managed according to the principles adopted by the association are expelled or forced to conform. Knowing the risks, the association ought to be in a position to see that no depositor ever loses a dollar.

There are two main objections to the plan. Some say that the jealousy and distrust among neighboring bankers makes it impossible to get bankers to co-operate in this way. This objection was raised when the system was first proposed for city bankers. Some of the city bankers were slow to join, but all managers of large city banks are now thoroly convinced that the plan has materially advanced their welfare. The bankers' opposition can not be well founded, because any plan to strengthen the banking system benefits the largest as well as the smallest bank.

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[37] The Way to Sounder Banking, by C. B. Hazelwood, *American Bankers Association Journal,* p. 256. October, 1925.

It may also be objected that as banks operate on a narrow margin, few could afford to join a country clearing-house association. If we assume an association with 25 member banks with each bank contributing $250 annually, a fund of $6,250 would be provided—an amount sufficient to hire a good manager and a stenographer. It is doubtful if $250 could be used in any other way to purchase as much protection, confidence, and good will. It is claimed that membership in a city clearing house has increased deposits, and it should increase deposits in country banks even more. The probable benefits of the clearing-house organization seem to more than justify the expense.

The country clearing-house plan, then, ought to reduce risks and losses, increase profits in banking, and at the same time help to meet the rather insistent demands of those interested in the integration of banks through branch banking. It has possibilities of being an effective and sensible solution of the present demand for guaranty of individual bank deposits.

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APPENDIX

TABLE I

NUMBER AND AMOUNT OF MORTGAGE LOANS, FORECLOSED LOANS, AND DELINQUENT INSTALLMENTS HELD BY MINNESOTA DEPARTMENT OF RURAL CREDIT, DECEMBER 31, 1926

County	Mortgage loans		Delinquent installments		Foreclosed loans	
	Number	Amount	Number	Amount	Number	Amount
Aitkin	325	$ 758,600	46	$ 6,451	4	$ 8.538
Anoka	88	311,900	9	2,025	none	
Becker	312	1,631,100	60	18,897	11	80,516
Beltrami	243	493.700	45	6,492	6	19,605
Benton	21	95,900	1	194	none	
Big Stone	31	234,100	9	3,797	none	
Blue Earth	30	275,100	1	200	none	
Brown	32	322,500	none		none	
Carlton	156	306,300	13	1,309	3	5,126
Carver	17	142,700	3	569	none	
Cass	334	736,600	53	5,710	17	52,466
Chippewa	46	412,200	1	406	2	18,680
Chisago	110	540,000	6	775	2	15,425
Clay	162	1,116,000	21	7,664	4	25.499
Clearwater	307	1,055,100	50	9,889	6	29,592
Cook	none		5	1,462	none	
Cottonwood	39	420,000	none		none	
Crow Wing	130	373,900	8	1,758	none	
Dakota	74	356,100	24	4,682	4	12,152
Dodge	25	215,100	none		none	
Douglas	79	521 800	12	4,580	none	
Faribault	36	408,200	7	2,440	none	
Fillmore	17	158,500	2	1,164	none	
Freeborn	30	282,700	2	559	none	
Goodhue	7	43,800	none		none	
Grant	82	630,700	4	985	none	
Hennepin	61	244,100	5	2,341	none	
Houston	11	88,700	1	252	1	7,714
Hubbard	133	367,800	15	2,241	1	4,721
Isanti	162	634,900	9	1,327	1	2,863
Itasca	98	218,700	10	802	none	
Jackson	30	338,900	5	1,741	none	
Kanabec	204	779,600	22	3,244	1	5,518
Kandiyohi	50	345,300	3	1,489	1	9,084
Kittson	338	1,785,500	70	22,322	18	97,395
Koochiching	45	77,800	3	220	none	
Lac qui Parle	56	555,100	3	1,938	none	
Lake	3	6,200	none		none	
Lake of the Woods	152	229,800	28	2,881	none	
LeSueur	17	120,500	none		none	
Lincoln	77	771,800	8	3,079	none	
Lyon	56	608,600	4	932	none	
McLeod	8	75,500	none		none	
Mahnomen	170	844,700	41	14,829	5	50,885
Marshall	605	2,710.700	114	37,154	34	223,877
Martin	23	242,300	1	375	none	
Meeker	34	259,100	none		none	

TABLE I—*Continued*

Number and Amount of Mortgage Loans, Foreclosed Loans, and Delinquent Installments Held by Minnesota Department of Rural Credit, December 31, 1926

County	Mortgage loans		Delinquent installments		Foreclosed loans	
	Number	Amount	Number	Amount	Number	Amount
Mille Lacs	93	338,600	5	1,100	1	3,259
Morrison	141	650,500	10	2,679	2	25,226
Mower	5	53,500	none		none	
Murray	28	305,200	7	3,803	none	
Nicollet	28	175,700	none		none	
Nobles	6	49,600	none		none	
Norman	140	842,100	27	6,507	4	48,992
Olmsted	4	32,700	none		none	
Ottertail	375	2,065,400	26	6,158	1	4,929
Pennington	317	1,498,000	82	21,514	28	171,859
Pine	280	813,800	20	3,522	2	18,281
Pipestone	6	53,500	1	936	none	
Polk	490	2,949,000	63	20,476	13	141,132
Pope	63	481,100	11	5,093	none	
Ramsey	29	107,400	4	459	none	
Red Lake	210	880,800	24	8,854	7	35,205
Redwood	23	237,500	3	1,547	none	
Renville	75	694,100	7	3,209	none	
Rice	6	48,900	none		none	
Rock	3	29,000	none		none	
Roseau	536	1,521,400	87	13,356	12	45,444
St. Louis	65	132,000	8	751	none	
Scott	36	287,000	6	1,707	none	
Sherburne	93	343,600	6	2,050	none	
Sibley	10	111,500	1	287	none	
Stearns	66	460,800	7	1,899	1	4,833
Steele	7	76,000	none		none	
Stevens	45	382,200	1	188	none	
Swift	102	907,000	20	6,727	1	7,555
Todd	161	839,400	10	2,398	none	
Traverse	45	355,300	5	3,173	1	10,336
Wabasha	21	172,100	5	1,097	none	
Wadena	179	747,300	34	5,744	2	7,845
Waseca	11	84,700	none		none	
Washington	77	449,700	15	5,161	none	
Watonwan	14	128,100	none		none	
Wilkin	38	325,700	2	432	1	7,560
Winona	24	222,300	1	2	2	18,454
Wright	30	187,100	3	1,000	none	
Yellow Medicine	25	260,500	1	619	none	

TABLE II

Direct Loans of the Twelve Federal Intermediate Credit Banks to Co-operative Marketing Associations, Close of Business December 31, 1927

District	Tobacco, Beans (a) Red-top seed (b)	Wheat, Dried fruit (c)	Cotton, Alfalfa seed (d) Raisins (e)	Wool
Springfield	$ 50,000	....	....	....
Baltimore	2,298,198	....	....	....
Columbia	....	....	$2,665,000	....
Louisville	1,950,409	....	....	....
New Orleans	....	....	4,880,721	....
St. Louis	51,600(b)	....	658,210	....
St. Paul	....	$ 826,682	....	$ 1,166
Omaha	....	550,000	....	209,970
Wichita	....	1,160,000	5,240,000	43,745
Houston	....	....	1,500,000	....
Berkeley	250,000(a)	407,705(c)	5,950,000(e)	21,055
Spokane	60,000(a)	37,400(c)	54,000(d)	135,506

District	Canned fruits and vegetables	Rice, Honey (f)	Total direct loans
Springfield	....	....	$ 50,000
Baltimore	....	....	2,298,198
Columbia	....	....	2,665,000
Louisville	....	....	1,950,409
New Orleans	....	....	4,880,721
St. Louis	....	$ 659,238	1,369,048
St. Paul	$ 20,000	....	847,848
Omaha	....	....	759,970
Wichita	....	....	6,443,745
Houston	....	....	1,500,000
Berkeley	611,241	1,155,646	8,395,647
Spokane	511,149	31,945(f)	830,009

TABLE III

Percentage of Tenancy in Minnesota and Neighboring States Compared, 1890-1925

Area	Percentage of farms rented				
	1925	1920	1910	1900	1890
Minnesota	27.1	24.7	21.0	17.3	12.9
North Dakota	34.4	25.6	14.3	8.5	6.9
South Dakota	41.5	34.9	24.8	21.8	13.2
Montana	21.4	11.3	8.9	9.2	4.8
Iowa	44.7	41.7	37.8	34.9	28.1
Wisconsin	15.5	14.4	13.9	13.5	11.4
Illinois	42.0	42.7	41.4	39.3	34.0
East north central states	26.0	28.1	27.0	26.3	22.8
West north central states	37.8	34.2	30.9	29.6	24.0
United States	38.6	38.1	37.0	35.0	28.4

TABLE IV

AMORTIZATION PLAN USED BY FEDERAL LAND BANK

Principal $1000 Rate 5% Semi-Annual Installments $30.00 Final Installment $46.58

Amortization table

Year due	No.	Interest*	Principal*	Date paid	Initial	Balance
1920	1	$25.00	$ 5.00	—	—	$995.00
1920	2	24.88	5.12	—	—	989.88
1921	3	24.75	5.25	—	—	984.63
1921	4	24.62	5.38	—	—	979.25
1922	5	24.48	5.52	—	—	973.73
1922	6	24.34	5.66	—	—	968.07
1923	7	24.20	5.80	—	—	962.27
1923	8	24.06	5.94	—	—	956.33
1924	9	23.91	6.09	—	—	950.24
1924	10	23.76	6.24	—	—	944.00
1925	11	23.60	6.40	—	—	937.60
1925	12	23.44	6.56	—	—	931.04
1926	13	23.28	6.72	—	—	924.32
1926	14	23.11	6.89	—	—	917.43
1927	15	22.94	7.06	—	—	903.13
1927	16	22.76	7.24	—	—	903.13
1928	17	22.58	7.42	—	—	895.71
1928	18	22.39	7.61	—	—	888.10
1929	19	22.20	7.80	—	—	880.30
1929	20	22.01	7.99	—	—	872.31
1930	21	21.81	8.19	—	—	864.12
1930	22	21.60	8.40	—	—	855.72
1931	23	21.39	8.61	—	—	847.11
1931	24	21.18	8.82	—	—	838.29
1932	25	20.96	9.04	—	—	829.25
1932	26	20.73	9.27	—	—	819.98
1933	27	20.50	9.50	—	—	810.48
1933	28	20.26	9.74	—	—	800.74
1934	29	20.02	9.98	—	—	790.76
1934	30	19.77	10.23	—	—	780.53
1935	31	19.51	10.49	—	—	770.04
1935	32	19.25	10.75	—	—	759.29
1936	33	18.98	11.02	—	—	748.27
1936	34	18.71	11.29	—	—	736.98
1937	35	18.42	11.58	—	—	725.40
1937	36	18.13	11.87	—	—	713.53
1938	37	17.84	12.16	—	—	701.37
1938	38	17.53	12.47	—	—	688.90
1939	39	17.22	12.78	—	—	676.12
1939	40	16.90	13.10	—	—	663.02
1940	41	16.57	13.43	—	—	646.59
1940	42	16.24	13.76	—	—	635.83
1941	43	15.90	14.10	—	—	621.73
1941	44	15.54	14.46	—	—	607.27
1942	45	15.18	14.82	—	—	592.45
1942	46	14.81	15.19	—	—	577.26
1943	47	14.43	15.57	—	—	561.69
1943	48	14.04	15.96	—	—	545.73
1944	49	13.64	16.36	—	—	529.37
1944	50	13.23	16.77	—	—	512.60

* The columns headed "Interest" and "Principal" show the portion of each $30 amortization installment applied on interest and principal, respectively. The amount taken for interest becomes less with each successive payment, while the amount on the principal increases each time. The balance column shows the debt remaining after each installment has been paid. It is entirely extinguished with the 72nd payment (36 years).

TABLE IV—*Continued*

AMORTIZATION PLAN USED BY FEDERAL LAND BANK

Principal $1000 Rate 5% Semi-Annual Installments $30.00 Final Installment $46.58

Amortization table						
Year due	No.	Interest*	Principal*	Date paid	Initial	Balance
1945	51	12.81	17.19			495.41
1945	52	12.38	17.62			477.79
1946	53	11.94	18.06			459.73
1946	54	11.49	18.51			441.22
1947	55	11.03	18.97			422.25
1947	56	10.56	19.44			402.81
1948	57	10.07	19.93			382.88
1948	58	9.57	20.43			362.45
1949	59	9.06	20.94			341.51
1949	60	8.54	21.46			320.05
1950	61	8.00	22.00			298.05
1950	62	7.45	22.55			275.50
1951	63	6.89	23.11			252.39
1951	64	6.31	23.69			228.70
1952	65	5.72	24.28			204.42
1952	66	5.11	24.89			179.53
1953	67	4.49	25.51			154.02
1953	68	3.85	26.15			127.87
1954	69	3.20	26.80			101.07
1954	70	2.53	27.47			73.60
1955	71	1.84	28.16			45.44
1955	72	1.14	45.44			

* See footnote, p. 97.

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University of Minnesota
Agricultural Experiment Station

The Tiger Beetles of Minnesota

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Division of Entomology and Economic Zoology

and

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UNIVERSITY FARM, ST. PAUL

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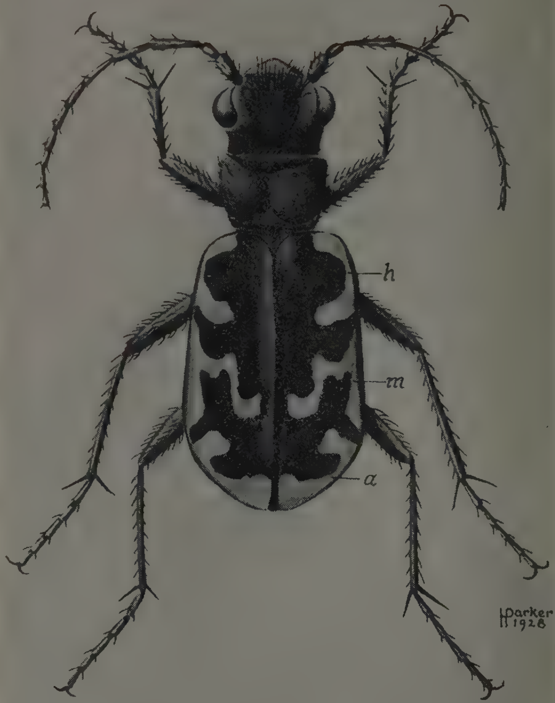
TIGER BEETLE
(Cicindela repanda)



h - humeral lunule
m - median band
a - apical lunule

BIOLOGY OF THE TIGER BEETLES WITH A KEY TO THE SPECIES OF CICINDELA FOUND IN MINNESOTA

R. W. Dawson

Few groups of insects, aside from the butterflies, have proved so interesting and attractive to amateur students as the tiger beetles. This is particularly true of the type genus, *Cicindela,* which is the dominant or major one in the family. This brief review of the tiger beetles of Minnesota is offered in the hope that it may afford one of the early stepping stones for the development of an interest in the study of insects.

The beginner, as well as the advanced student, finds the tiger beetles an attractive group for several reasons. They are neatly marked and beautifully, even gorgeously, colored. Their beauty, along with the ease and certainty with which specimens may be preserved in perfect condition, renders them more than usually satisfactory material for the building of a collection.

The variety of forms is relatively large. Seventy-six species and 102 varieties are at present cataloged for the United States and Canada. The recognition and correct separation of all these forms constitutes a challenge to the student, and herein lies the first absorbing interest in the tiger beetles. The pursuit of this taxonomic interest tends strongly to lead one into some of the great modern problems of biology, namely, ecology, genetics, and evolution, for only by the aid of these fundamental fields of study can one hope to settle the more difficult and obscure questions in classification.

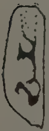
The frontispiece illustrates the generalized, or type, pattern of markings characteristic of the North American tiger beetles. The "idea" of this color pattern runs through the whole genus. The color design of all the species may be derived from this pattern by relatively simple modifications of its parts. These parts, as the plate shows, consist of the humeral lunule, median band, apical lunule, and marginal band. These elements show a homology almost as precise and definite as do the bones of a series of vertebrate animals. The evidence from homologies is one of the great categories of facts supporting the theory of evolution. That even such a superficial character as color markings should show definite homologies is a remarkable and interesting fact. To illustrate it the plate showing the elytra of the various local forms has been arranged as a graded series to show how the modifications may progress. The real relationships of the species and varieties are not shown by this character alone, and the plate, therefore, does not reflect an evolutionary series, but shows the homologies of the color patterns, and aids in making identifications.

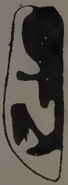
In the days of Linnaeus, the first great classifier of plants and animals, the universally accepted idea was that species were separately or "specially" created, each distinct, fixed, and unchanging. Echoes of this idea still persist. It becomes, then, an item of peculiar interest that no group of common animals gives more striking and absorbingly interesting evidence bearing upon this question of the fixity of species than does the group of tiger beetles. Nearly every species has a valid, named variety, and sometimes several of them. Many of the varieties show every step of gradation in the transition from the one to the other; and when some of the complete transitional series are assembled one is amazed at their range and at the definiteness with which the variations are correlated with seasons, habitats, and geographical distribution.

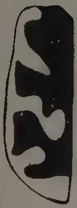
The student of ecology may find much of interest in the tiger beetles. The plastic nature of their colors and markings renders them peculiarly appropriate material for the study of variations induced by climatic and physical factors—temperature, moisture, light, soil types, and others. In a general way, higher temperatures tend to reduce the strength (area) of the pale markings of the elytra, and lower temperatures tend to augment the pale markings. Similarly, brilliance of color is suppressed by moisture and brought to full expression by dryness, The segregation of the various species and varieties to particular soil types and moisture conditions is rather definite.

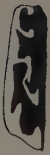
Life histories and habits constitute another phase of the ecological aspect of the study. The species are all predacious, and are so active and aggressive in character as to well deserve the name "tiger" beetle. Any small creature, caterpillar, fly, ant, or even spider, is appropriate prey. The prey is fiercely pounced upon and devoured with avidity. The beetles are very nimble and agile, they run and hide with great facility and take wing upon slight provocation.

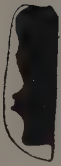
The larvae, also, are predacious. They occur in the same local habitats as the adult beetles—clay banks, sand pits, sandy beaches of lakes and streams, roads, woodland paths, and bare spots of ground. For the most part they dig essentially perpendicular burrows in which to live, and secure their prey by resting at the top of the burrow. The flattened top of the head and front segment of the thorax nearly fill and close the mouth of the burrow. The unsuspecting insect pedestrian is suddenly seized by the large, powerful jaws and dragged into the burrow to be devoured. The tiger beetle larva is protected by the armor on top of the flattened head and prothorax, and the victim is at a complete disadvantage. The remainder of the larva's body, which is protected by the walls of the burrow, is soft and delicate.

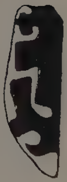

lepida

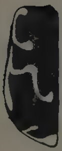

manitoba

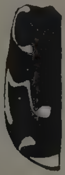

generosa


cuprascens


lecontei


hirticollis


repanda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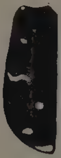
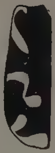
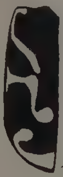
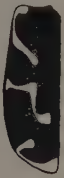
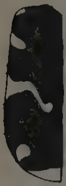
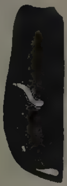

12-guttata

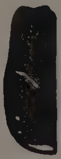

fulgida

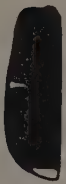

kirbyi

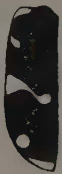

tranquebarica

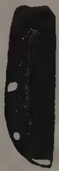

limbalis


graminea


auduboni


splendida


patruela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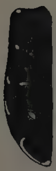
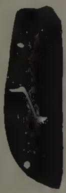
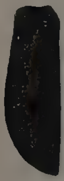
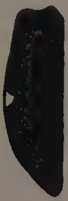
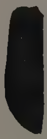

punctulata


longilabris


nebraskana


unipunctata


pusilla

A pair of dorsal prominences, or hooks, enables the larva more readily to maintain its strategic position at the top of the burrow. An interesting demonstration of these larvae and their burrows may often be had where they are common by standing quietly for a few minutes, then suddenly stamping upon the ground, or moving the arm so as to cast a wave of shadow across the bare ground. The sudden dropping of all the tiger beetle larvae from the mouths of their burrows seems magically to perforate the ground with numbers of sharply outlined round holes. After a few moments of quiet the holes unobtrusively disappear as they are "plugged" one after another by the heads of the occupants.

The life cycle of *Cicindela purpurea* has been summarized by Shelford (5), at Chicago, as follows: Eggs are laid in May; larvae reach the last (third) stage in August, hibernate, begin to feed again in April, and pupate in July. The adults emerge in August, feed for a time, hibernate, and come out in the second spring, reach sexual maturity in the first warm days of April, and soon begin depositing eggs. Upon the completion of this function they die. The larval life thus lasts from 12 to 13 months and the adult life 10 months. This makes a two-year life cycle. Criddle (1), at Aweme, Manitoba, finds that two years are required there for the larval development, and that therefore three years are required for the life cycle. As the broods overlap, specimens are to be seen in essentially equal numbers every year. One of our common species, *C. punctulata,* apparently has an annual cycle in the region of Chicago.

The depth of the burrows of tiger beetles and their larvae varies greatly, from a few inches to 6½ feet, depending upon the species, temperature, moisture, and type of soil. The deep burrows are for winter hibernation (recorded by Criddle, in Manitoba).

Something of the interest that has long attached to this group of insects may be gleaned from the following quotation from Dow (2). "When the news reached London that Say had caught a tiger beetle an inch and one-half long, of a new genus, an enthusiast bid $300 gold for the specimen, and Say accepted it. Both sides were quite satisfied, for as luck would have it, a second specimen was not captured until about twenty years later." Again: The beautiful species *C. limbata* was lost to science for a number of years after Say described it. When rediscovered, specimens were so much in demand by collectors and students that several collecting expeditions were financed by the sale of specimens, until the world market was supplied. The "golden days" are past. There is no money in tiger beetles, but these incidents help one to realize the interest that has long centered upon these attractive insects.

KEY TO THE SPECIES OF MINNESOTA TIGER BEETLES

1. Front entirely bare (except for the few erect orbital bristles that are present in all species) 2
Front clothed (at least sparsely) with hairs 8

2. Color brilliant green, blue, purple, or changeable green to blue and purple 3
Color black, dull black, or at most with a bronzed or purplish sheen 4

3. Immaculate or with traces of normal markings in the form of three white dots on each elytron.......... *sexguttata* Fabricus
Strongly marked, humeral and apical lunules interrupted at the middle but median band complete .... *sexguttata* subsp. *patruela* Dejean

4. Front with a well-marked depression or dent between the eyes; depression limited below by a distinct transverse elevation 5
Front without a well-marked depression or dent between the eyes 6

5. Surface luster duller, color brownish black; normal markings more or less well indicated .... *longilabris* Say
Surface shining black; pale markings suppressed .... *longilabris* var. *nebraskana* Casey

6. Sides of thorax and abdomen beneath thinly clothed with pale hairs 7
Sides of thorax and abdomen beneath bare; body above flatter than usual; color opaque black, showing a marked violet sheen under a hand lens; elytra with a mid-lateral pale spot ....*unipunctata* Fabricius

7. Elytra with a row of large, metallic foveae or pits near the suture, and a short double row of the same near the humeral angles. Color blackish above with more or less evident blue, green, or purple reflections, and traces of normal pale markings; length 10-13 mm. ...... *punctulata* Oliv.
Elytra without large, metallic foveae; color usually dull black with or without pale markings; size small, length about 10 mm. ......*pusilla* Say

8. Antennae and legs pale testaceous; creamy white markings of elytra very broad, partially confluent, so that the prevailing color of the elytra is creamy white ....*lepida* Dejean
Antennae and legs dark, or brilliantly metallic; creamy white markings of elytra absent to very strong and bold, but never dominating the general color tone of the insect 9

9. Front, middle, and almost always hind trochanters, and sometmies tibiae also, testaceous 10
Legs without any testaceous coloring, entirely bright metallic like body ... 11

10. Elytra brilliant cupreous, strongly and densely punctured, pale markings very distinct ....*cuprascens* Leconte
Elytra less brilliant, bronzed rather than cupreous, less strongly punctured, markings narrower and less distinct .... *cuprascens* var. *macra* Leconte

11. Pale markings of elytra confined to an irregular submarginal band, often more or less interrupted, and evidently formed by the coalescence of the lateral portions of the typical pale markings; color varying, dull cupreous to bronzed ...*scutellaris* subsp. *lecontei* Hald.
Pale markings of elytra not confined to the sides in the form of an irregular band 12

12. General color above red, green, or black 13
General color above dull brown, bronzed brown, or blackish brown; pale markings usually complete, or typical 17

13. Smaller, slenderer species, length 11-12 mm.; color above in different individuals varying from a very brilliant light red to a deep blackish red, surface polished or shining .... *fulgida* Say
Larger, more robust species; length 13-15 mm.; surface less polished and less shining 14

14. Head and pronotum brilliant green, blue, or purple in marked contrast to the red elytra; pale markings much reduced .... *purpurea* subsp. *splendida* Hentz
Head and pronotum not colored in marked contrast to the elytra 15

15. Color uniformly black, except for traces of the typical pale markings .... *purpurea* var. *auduboni* Leconte
Color red or green, head and pronotum with coppery reflections 16

16. Green above, lateral margins of elytra with coppery reflections; median pale bland oblique and well marked .... *purpurea* var. *graminea* Schpp.
Red above; margins of elytra green or blue with traces of coppery reflections; pattern of pale markings often nearly complete .... *purpurea* subsp. *limbalis* Klug.

17. Posterior third of humeral lunule bent abruptly inward and directed slightly forward; elytra with sides more bulging than usual and their apex more distinctly produced .... *hirticollis* Say
Posterior third of humeral lunule bent obliquely inward, never so abruptly as to be directed anteriorly 18

18. Smaller species, length 11-13 mm. 19
Larger species, length 13-19 mm. 21

19. Markings slenderer, usually broken into dots, middle band usually not at all extended on the lateral margin .... *duodecimguttata* Dejean
Markings broader, usually not interrupted; median band more or less extended along the lateral margins of the elytra 20

20. Color dark brown; form relatively broader and shorter; pronotum relatively narrower in proportion to the width of the head; pale markings stronger, middle band more extended on the margin, approaching or even uniting with the humeral lunule .... *duodecimguttata* subsp. *repanda* Dejean
Color blackish brown; form relatively more elongate; pronotum broader in proportion to the width of the head; pale markings narrower, the median band less extended on the elytral margin, and not closely approaching the humeral lunule .... *duodecimguttata* var. *bucolica* Casey

21. Pale markings bold and heavy, broadly connected on the elytral margins 23
Pale markings not connected laterally 22

22. Bright bronze, thorax cupreous, lunule entire .... *tranquebarica* subsp. *horiconensis* Leng
Dull bronze, markings heavy, humeral lunule very long, almost touching the median band .... *tranquebarica* subsp. *kirbyi* Leconte
Darker, more blackish brown, markings narrower, humeral lunule shorter *tranquebarica* Hbst.

23. Elytral markings exceptionally strong and bold; pale hairs somewhat more densely placed and more conspicuous .... *formosa* race *manitoba* Leng
Elytral markings less strongly developed; pale hairs less dense and conspicuous .... *formosa* subsp. *generosa* Dejean

NOTES AND RECORDS ON THE TIGER BEETLES OF MINNESOTA

Walther Horn

Deutsches Entomologisches Institut, Berlin-Dahlem, Germany

The Division of Entomology and Economic Zoology, University of Minnesota, was kind enough to send me for study the material of the Cicindelidae of the world belonging to their insect collection. As the fauna of Minnesota is especially well represented in this lot, I give herewith a list of them. I have added some species not represented in the material sent to me, but known to me as occurring in Minnesota.

1. *Cicindela formosa* subsp. *generosa* Dejean

Localities represented: Anoka County, Fridley sand dunes, June 1, 1922 (Wm. E. Hoffmann); Anoka County, Fridley sand dunes, July 14, 1922 (A. A. Nichol); Anoka County, Fridley sand dunes, August 8, 1922 (C. Johnson); Hennepin County, May 24, 1920 (Wm. C. Cook); Ramsey County, New Brighton, June 30, 1922 (C. E. Mickel); Ramsey County, July 13, 1910; Scott County, Barden sand dunes, July 29, 1923 (R. W. Dawson); Scott County, dunes near Jordan, August 1 (Wm. E. Hoffmann); Scott County, sand dunes, August 25, 1922 (A. A. Nichol); Washington County, August 13.

2. *Cicindela formosa* race *manitoba* Leng

The following specimens are intermediate in form, more or less related to the Canadian race "*manitoba* Leng:"

Localities represented: Anoka County, Fridley sand dunes, August 8, 1922 (C. Johnson); Scott County, Barden sand dunes, August 25, 1922 (C. E. Mickel); Scott County, Jordan sand area, July 23, 1923 (H. H. Knight); Ramsey County; Scott County, Barden sand dunes, July 29, 1923 (R. W. Dawson).

3. *Cicindela pūrpurea* Olivier

Localities represented: Clearwater County, Itasca Park, August 15-30, 1921 (H. L. Person); Clearwater County, Lake Itasca, May 27, 1911; Clearwater County, Lake Itasca, June, 1911; Ottertail County, May 24; Ramsey County, St. Anthony Park, St. Paul, May 10, 1909; St. Louis County, Tower.

4. *Cicindela purpurea* var. *auduboni* Leconte

The black form, *auduboni* Leconte 1856 (!) = *spreta* Leconte 1856 (!) is represented by one specimen from Ramsey County.

5. *Cicindela purpurea* var. *graminea* Schpp.

The greenish form, *auduboni* Leconte 1845 (!) = *graminea* Schpp. 1883/4 is represented by one specimen from Ramsey County, 1917.

6. *Cicindela purpurea* subsp. *splendida* Hentz

This species is known to me from an unrecorded locality in the state of Minnesota.

7. *Cicindela purpurea* subsp. *limbalis* Klug.

Localities represented: St. Louis County, Duluth; Clearwater County, Itasca Park, June 12, 1914; Itasca County; Clearwater County, Itasca Park, August 15-30, 1921 (H. L. Person); Norman County, March 30; Ottertail County.

8. *Cicindela duodecimguttata* Dejean

Localities represented: Renville County, Bird Island, August 25, 1921 (Wm. E. Hoffmann); Clearwater County, Itasca Park, August 15-30 (H. L. Person); St. Louis County, August 13, 1910.

9. *Cicindela duodecimguttata* var. *bucolica* Casey

In this variety the single lunules are not interrupted (*bucolica* Casey = *edmontonensis* Carr.).

Localities represented: Anoka County, June 5, 1920; Lake County, Baptism Creek, August 21, 1920 (H. H. Knight); Lake County, Bengal, August 18, 1922 (H. H. Knight); Big Stone County, July 20, 1911; Renville County, Bird Island, August 25, 1921 (Wm. E. Hoffmann); Cook County, Cascade River, August 14 (H. H. Knight); Hennepin County, Crystal Lake, July 30, 1921 (A. T. Hertig and H. H. Knight); Rice County, Faribault, June 20, 1922 (Wm. E. Hoffmann); Hennepin County, July 6, 1910; Hubbard County, N. E. corner Itasca Park, August 22, 1922 (Wm. E. Hoffmann); Clearwater County, Itasca Park, July 1-13, and August 4-30, 1921 (H. L. Person); Lesueur County, Fish Hatchery, July 22, 1923 (Sam Kepperley); Lesueur County, July 25, 1922 (R. R. Holland); Nicollet County, September 7, 1923 (Wm. E. Hoffmann); St. Louis County, August 27, 1910; Nicollet County, St. Peter, Fish Hatchery, August 11, 1923 (Sam Kepperley); Chisago County, Taylors Falls, August 5, 1922 (H. H. Knight); Wilkin County, August 14, 1912.

10. *Cicindela duodecimguttata* subsp. *repanda* Dejean

Localities represented: Anoka County, August 9, 1920 (H. H. Knight); Beltrami County, August 9, 1910; Renville County, Bird Island, August 25, 1921 (Wm. E. Hoffmann); Hennepin County, Crystal Lake, July 30, 1921 (A. T. Hertig); Hennepin County, April 22, June 10, and July 6; Hennepin County, Lake Independence, July 30, 1918; Hennepin County, May 24, 1920 (Wm. C. Cook); Houston County, June 15, 1910; Clearwater County, Itasca Park, July 1-13, and August 15-30, 1921 (H. L. Person); Washington County, Newport, July 18, 1922 (C. E. Mickel); Steele County, Owatonna, Straight River, June 22, 1922 (Wm. E. Hoffmann); Ramsey County; Ramsey County, Battle Creek, May 20, 1922 (C. E. Mickel); Ramsey County, June 25, 1921 (H. H. Knight); Sibley County, river near Blakeley, July

17, 1922 (Wm. E. Hoffmann); Ramsey County, St. Anthony Park, St. Paul, April 20; Nicollet County, St. Peter, July 20, 1922 (A. T. Hertig); Nicollet County, St. Peter, near Fish Hatchery, August 11, 1923 (Sam Kepperley).

11. *Cicindela hirticollis* Say

Localities represented: Ramsey County, Gray Cloud Island, July 12, 1921 (Wm. E. Hoffmann).

12. *Cicindela tranquebarica* Hbst. = *vulgaris* Say

Localities represented: Scott County, Barden sand dunes, August 25, 1925 (C. E. Mickel); Renville County, Bird Island, August 25, 1921 (Wm. E. Hoffmann); Clearwater County, Itasca Park, August 15-30, 1921 (H. L. Person); Clearwater County, Lake Itasca, May 25, June 3, 1914 (on sand heap, running), June 21, and August 12; Ottertail County, May 24; Cass County, Pillager, September 14, 1918 (V. R. Haber); Ramsey County, Gray Cloud Island, July 12, 1921 (Wm. E. Hoffmann); Scott County, sand dunes, August 25, 1922 (A. A. Nichol); Scott County, Shakopee, June 10, 1922 (C. E. Mickel); St. Louis County, Tower.

13. *Cicindela tranquebarica* subsp. *kirbyi* Leconte

The following specimens are intermediate in form, the middle band is enlarged near the lateral border (more or less resembles subsp. *kirbyi* Leconte).

Localities represented: Clearwater County, Itasca Park, August 15-30, 1921 (H. L. Person); Clearwater County, Lake Itasca, May 1; Ottertail County, August 21; Scott County, sand dunes, August 25, 1922 (A. A. Nichol).

14. *Cicindela tranquebarica* subsp. *horiconensis* Leconte

This subspecies is known to me from an unrecorded locality in the state of Minnesota.

15. *Cicindela longilabris* Say

Localities represented: Lake County, Baptism Creek, August 21, 1920 (H. H. Knight); Lake County, Bengal, August 18, 1922 (H. H. Knight); Carlton County, May 20, 1911; Cook County, Cascade River, August 14, 1922 (H. H. Knight); St. Louis County, Duluth; Clearwater County, Itasca Lake, June 27, 1911; Clearwater County, Itasca Park, August 15-30, 1921 (H. L. Person); Lake County, Kawishiwi River, August 30, 1919 (H. H. Knight); Roseau County, Clear River, June 29, 1920.

16. *Cicindela* var. *nebraskana* Casey

Blackish specimens without or almost without pattern.

Localities represented: Clearwater County, Itasca Lake, June 8, 1914; Crow Wing County, Nisswa, July 6, 1922 (Wm. E. Hoffmann).

17. *Cicindela fulgida* Say

This species is known to me from an unrecorded locality of the State of Minnesota.

18. *Cicindela scutellaris* subsp. *lecontei* Hald. = *modesta* Dejean 1825 (!)

Localities represented: Hennepin County; Ottertail County; Hennepin County, Fort Snelling, High Prairie, April 29, 1921 (R. N. Chapman).

19. *Cicindela sexguttata* Fabricius

Localities represented: Hennepin County, basswood-maple forest, July 21, 1922 (A. A. Nichol); Ramsey County; Ramsey County, St. Anthony Park, St. Paul, June 1, 1921 (H. H. Knight); Nicollet County, St. Peter, Fish Hatchery, July 22 (Wm. E. Hoffmann); Chisago County, Taylors Falls, June 23, 1920 (B. Kienholz).

20. *Cicindela sexguttata* subsp. *patruela* Dejean

The following Minnesota records were generously furnished by Professor Myron H. Swenk, Department of Entomology, University of Nebraska.

Localities represented: Crow Wing County, Pelican Lake, Nisswa, July 14, 20, 22, 23, 27, 28, and 30, 1912, and August 10 and 11, 1912 (L. Bruner).

21. *Cicindela punctulata* Olivier

Localities represented: Freeborn County, Albert Lea, July 10, 1923 (P. L. Keene); Anoka County, Fridley sand dunes, July 14, 1925 (C. E. Mickel); Hennepin County, July 6, 1910; Clearwater County, Itasca Park, August 4-30, 1921 (H. L. Person); Chisago County, North Branch, August 6, 1922 (Wm. E. Hoffmann); Scott County, dunes near Jordan, August 1, 1922 (Wm. E. Hoffmann); Hennepin County, Fort Snelling, August 27, 1924 (Allen McIntosh); Ramsey County, St. Anthony Park, St. Paul, August 1, 1920 and July 9, 1921 (H. H. Knight); Ramsey County, St. Paul, July 11, 1925, at light (Sam Kepperley).

22. *Cicindela pusilla* Say

Localities represented: Chisago County, July 16, 1911; Hennepin County; Ottertail County; Ramsey County; Red Lake County, August 1, 1923 (C. E. Mickel).

23. *Cicindela unipunctata* Fabricius

This species is known to me from an unrecorded locality of the State of Minnesota.

24. *Cicindela cuprascens* Leconte

This species is known to me from an unrecorded locality of the State of Minnesota.

25. *Cicindela cuprascens* subsp. *macra* Leconte

Localities represented: Scott County, Jordan sand area, July 13, 1923 (H. H. Knight); Ramsey County, Gray Cloud Island, July 12, 1921 (Wm. E. Hoffmann).

26. *Cicindela lepida* Dejean

Localities represented: Anoka County, Fridley sand dunes, August 3-8, 1924 (R. W. Dawson); Anoka County, Fridley sand dunes, July 14, 1922 (A. A. Nichol); Scott County, Jordan sand area, July 13, 1923 (H. H. Knight).

In addition to the species listed above there are two others: *Cicindela lengi* W. H. (= *venusta* Leconte) and *C. limbata* Say, which might occur in the state, altho there are no known records of these species from Minnesota.

Considering this group of species as a whole, there are three features of general interest: (1) All the forms belong to groups in which the four anterior trochanters bear so-called "fixed" hairs (W. Horn [3] in Wytsman's *Genera Insectorum,* Cicindelinae, 1908-15, p. 214). (2) If the Minnesota forms are compared with all of the Cicindelidae of the United States, or with those of the United States and Mexico, it will be noticed that all the Minnesota forms belong to groups in which the upper side of the head and pronotum bear bristles or hairs. I do not believe this is accidental, but think it may be a characteristic feature of the species found in northern localities. (3) The group of species represented here is a very restricted one, in my opinion, characteristic of northern regions.

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University of Minnesota
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UNIVERSITY FARM, ST. PAUL

TABLES FOR DETERMINING THE VOLUME OF BLACK SPRUCE[1]

R. M. Brown

Tree volume tables for black spruce, *Picea mariana,* based on data collected in Minnesota are not available. Black spruce is found in many swamps in the northern part of the state and is in great demand for pulpwood. The need for volume tables to estimate these stands has long been apparent.

The harvesting of a black spruce stand on the Cloquet Forest Experiment Station offered an opportunity for the necessary measurements for the preparation of such tables. This was a pure stand between 100 and 110 years old one foot from the ground. In general, it was similar to many black spruce stands occurring in swamps of northern Minnesota.

FIELD METHODS

Tree Measurements

The tree measurements upon which the volumes in the tables are based were taken during the winter of 1928. The diameters outside of bark were measured by means of calipers at one foot, 2, 3, 4.5, 9.15, 12, 17.3 feet above ground and at 8.15-foot intervals above the last measurement. Two diameters at right angles were measured at each point. Diameters inside the bark were obtained by measuring the bark thickness with a Swedish bark-measuring instrument. These diameter measurements were plotted directly in the field on U. S. D. A. Forest Service Tree Measurement Form 558a.

Cordwood Measurements

To obtain the solid contents of stacked pulpwood for converting the volume in cubic feet to volume in cords, trees were cut into 8-foot bolts and piled in 2x8x8-foot ricks. Six stacks of this size, the equivalent of six standard cords, were measured. The diameter outside of bark at the middle of each bolt was measured with calipers and the length was measured with a tape. Bark thickness was measured with a Swedish bark-measuring instrument. The diameter breast high of the tree from which each bolt was taken was recorded with each bolt measurement.

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[1] The study was carried on in co-operation with the Lake States Forest Experiment Station.

METHOD OF COMPILATION

Volume Tables

The volume in cubic feet of each tree was obtained by the planimeter method. The tables were made from these volumes by the alinement chart method.[2] For making cubic foot volume tables, this method consists in modifying the scale graduations of a cylinder volume alinement chart so the graduations represent the actual tree volumes.

Reliable volume tables can be made by this method with comparatively few trees, since the entire sample of data is used as the basis of a single curve. This curve usually approximates a straight line. Reliable extensions can therefore be made beyond the limits of the data.

Cordwood Converting Factors

To obtain the cordwood converting factors, the solid contents of each cord was determined by computing the volumes of the bolts by Huber's formula and totaling them.[3] These figures were analyzed to see whether the solid contents of a cord varied with a change in tree diameter. No relation was evident in the data, probably because of the limited range of diameters in the stand and the small number of stacks measured.

The average bolt diameter, solid contents, and number of bolts per cord (Table I) obtained from the six cords were then compared with similar data obtained by H. L. Churchill[4] for Adirondack spruce, to see if these figures could be applied to black spruce. The comparison showed a difference in solid contents and number of bolts of less than 1.5 per cent. This difference could easily have resulted from slight differences in piling. The converting factors for Eastern spruce, in combination with the average middle diameters of 8-foot bolts for trees of different sizes obtained from the original tree measurements, were therefore used to obtain the converting factors based on tree diameter. (See Table VI for the converting factors.)

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[2] Bruce, D., and Reineke, L., of the U.S.D.A. Forest Service, private communication.

[3] Volume in cubic feet is equal to the sectional area at the middle of the bolt in square feet multiplied by the length in feet.

[4] Chapman, H. H. "Forest mensuration." Table XXIV, p. 131. 1924.

TABLE I

AVERAGE DIAMETER BREAST HIGH OF TREES, BOLT DIAMETER, AND CONTENTS OF SIX CORDS* OF BLACK SPRUCE PULPWOOD, CLOQUET, MINNESOTA

D.B.H.	Trees per cord	Bolt diam. with bark†	4-foot bolts per cord	Solid contents per cord		Basis cords
				Wood	Wood and bark	
in.		in.		cu. ft.		
6.5	14.5	5.6	121	75	84	6

* Stack 2x8x8 feet, one-half double cord, or the equivalent space of a standard cord.

† Middle diameter.

The volumes in cords in Table VI were obtained by dividing the merchantable volumes in Table V by these converting factors.

Precision of Compilation

To determine how closely the volume tables represent the volumes of the trees from which the tables were made, the average deviation and aggregate difference in per cent were computed for each table. The average deviation in per cent is the average difference between each tree volume and the corresponding table volume expressed as a percentage of the average table volume. For these tables, the average deviation is less than 5 per cent. In other words, the individual tree volumes differ on an average from the table volumes by this percentage. The aggregate difference in per cent is the difference between the total of the actual tree volumes and the total of the corresponding table volumes as a percentage of the total of the table volumes. In the case of each table this error is less than 0.1 per cent. The specific percentages will be found in the footnotes of each table. These percentages show that the tables represent very closely the tree volumes from which they were made.

TABLE II
BLACK SPRUCE
(Picea mariana)
PEELED TOTAL STEM VOLUME*

R. M. Brown
R. Knudson

Minnesota
1928

I. Taylor
T. Lotti

Diameter breast high	Total height of tree—feet								Basis
	30	35	40	45	50	55	60	65	
Inches	Volume—cu. ft.								Trees
3									4
4	1.3	1.5	1.8	2.0	2.2				18
5	2.1	2.4	2.8	3.1	3.4	3.8			16
6		3.5	3.9	4.4	4.8	5.3	5.7	6.2	20
7			5.2	5.8	6.4	7.0	7.6	8.2	19
8			6.7	7.5	8.2	9.0	9.7	10.5	10
9				9.2	10.0	11.0	12.0	13.0	4
10				11.5	12.5	13.5	14.5	16.0	
11					15.0	16.0	17.5	19.0	
12					17.5	19.0	20.5	22.0	
Basis	1	2	8	12	22	21	19	6	91

* Volume includes stump, stem, and top without bark.

Data collected in 1928 by I. Taylor and T. Lotti.

Block indicates the range of basic data.

Average deviation of individual tree volumes from table volumes, ± 4.4 per cent.

Difference between sum of basic volumes and sum of corresponding table volumes, 0.02 per cent of table volumes.

TABLE III

BLACK SPRUCE

(Picea mariana)

UNPEELED TOTAL STEM VOLUME*

R. M. Brown
R. Knudson

Minnesota
1928

I. Taylor
T. Lotti

Diameter breast high	Total height of tree—feet								Basis
	30	35	40	45	50	55	60	65	
Inches	Volume—cu. ft.								Trees
3									4
4	1.5	1.7	2.0	2.3	2.5				18
5	2.4	2.7	3.1	3.5	3.8	4.2			16
6		3.9	4.4	4.9	5.4	5.9	6.4	6.9	20
7			5.8	6.5	7.2	7.9	8.5	9.2	19
8			7.5	8.3	9.2	10.0	11.0	11.5	10
9				10.5	11.5	12.5	13.5	14.5	4
10				12.5	14.0	15.0	16.5	17.5	
11						18.0	19.5	21.0	
12						21.0	23.0	25.0	
Basis	1	2	8	12	22	21	19	6	91

* Volume includes stump, stem, and top with bark.

Data collected in 1928 by I. Taylor and T. Lotti.

Block indicates the range of basic data.

Average deviation of individual tree volumes from table volumes, ± 3.7 per cent.

Difference between sum of basic volumes and sum of corresponding table volumes, 0.05 per cent of table volumes.

TABLE IV
BLACK SPRUCE
(Picea mariana)

PEELED MERCHANTABLE VOLUME*

R. M. Brown
R. Knudson

Minnesota
1928

I. Taylor
T. Lotti

Diameter breast high	Total height of tree—feet								Basis
	30	35	40	45	50	55	60	65	
Inches	Volume—cu. ft.								Trees
4	.9	1.1	1.4	1.7	1.9				18
5	1.8	2.2	2.6	2.9	3.3	3.6			16
6		3.3	3.9	4.4	4.9	5.4	5.8	6.3	20
7			5.3	5.9	6.6	7.2	7.8	8.5	19
8			6.8	7.6	8.4	9.2	10.0	11.0	10
9				9.6	10.5	11.6	12.5	13.5	4
10				11.5	13.0	14.0	15.5	16.5	
11					15.5	17.0	18.5	20.0	
12					18.0	20.0	21.5	23.5	
Basis			7	12	22	21	19	6	87

* Volume includes the stem without bark above a 1-foot stump to a 3-inch top diameter inside of bark.

Data collected in 1928 by I. Taylor and T. Lotti.

Block indicates the range of basic data.

Average deviation of individual tree volumes from table volumes, ± 4.6 per cent.

Difference between sum of basic volumes and sum of corresponding table volumes, ±0.04 per cent of table volumes.

TABLE V
BLACK SPRUCE
(Picea mariana)
UNPEELED MERCHANTABLE VOLUME*

R. M. Brown
R. Knudson

Minnesota
1928

I. Taylor
T. Lotti

Diameter breast high	Total height of tree—feet								Basis
	30	35	40	45	50	55	60	65	
Inches	Volume—cu. ft.								Trees
4	.8	1.0	1.2	1.5	1.7	......	......	......	18
5	1.6	1.9	2.3	2.6	3.0	3.3	......	......	16
6	......	3.0	3.5	3.9	4.4	4.8	5.2	5.7	20
7	......	......	4.8	5.3	5.9	6.5	7.0	7.6	19
8	......	......	6.1	6.8	7.6	8.3	9.0	9.8	10
9	......	......	......	8.6	9.5	10.5	11.5	12.5	4
10	......	......	......	10.5	11.5	13.0	14.0	15.0	......
11	......	......	......	......	14.5	15.0	16.5	18.0	......
12	......	......	......	......	16.5	18.0	19.5	21.0	......
Basis	......	......	7	12	22	21	19	6	87

* Volume includes the stem with bark above a 1-foot stump to a 3-inch top diameter inside of bark.

Data collected in 1928 by I. Taylor and T. Lotti.

Block indicates the range of basic data.

Average deviation of individual tree volumes from table volumes, ± 4.4 per cent.

Difference between sum of basic volumes and sum of corresponding table volumes, 0.01 per cent of table volumes.

TABLE VI

BLACK SPRUCE

(Picea mariana)

UNPEELED MERCHANTABLE VOLUME*

(Standard cords, 4×4×8 ft.)

R. M. Brown R. Knudson	Minnesota 1928	I. Taylor T. Lotti

Diameter breast high	Total height of tree—feet								Basis	Cordwood Converting Factors
	30	35	40	45	50	55	60	65		
Inches	Volume—cords								Trees	cu. ft.
4	012	.014	.018	.022	.024				18	78
5	.022	.027	.032	.035	.040	.044			16	82
6		.039	.046	.052	.058	.064	.069	.075	20	84
7			.062	.069	.077	.084	.091	.099	19	86
8			.078	.087	.097	.105	.115	.125	10	87
9				.110	.120	.130	.140	.155	4	88
10				.130	.145	.155	.175	.185		89
11					.170	.190	.205	.220		90
12					.200	.220	.240	.260		90
Basis			7	12	22	21	19	6	87	

* Volume includes the stem with bark above a 1-foot stump to a 3-inch top diameter inside of bark.

Volumes computed from unpeeled merchantable table by dividing by the converting factors given in the last column of the table.

Data collected in 1928 by I. Taylor and T. Lotti.

Block indicates the range of basic data.

Average deviation of individual tree volumes from table volumes, ± 4.4 per cent.

Aggregate difference, 0.01 per cent.

PRECAUTIONS TO BE TAKEN IN THE APPLICATION OF THE TABLES IN TIMBER ESTIMATING

The following precautions must be observed in the application of any volume table.

Applicability Check

The failure of the average volumes of given diameter and height classes of a volume table to correspond with the average volumes of the trees of the same sizes in the stand to be estimated is a common source of error in timber estimating. A volume table based on tree volumes from one locality should never be applied to stands in another locality before it has been checked against tree volumes obtained from the stands to be estimated. This comparison of the table volumes with the actual volumes of the trees in the stand to be estimated is known as the *applicability check.*

The procedure in making this check is as follows:[5]

> "In checking the applicability of volume tables, a relatively small number of trees may be used. If their aggregate difference and average deviation from the table be calculated, the test for satisfactory accuracy is:
>
> "(1) An average deviation of the same order of magnitude as that of the basic data on which the table was prepared.
>
> "(2) An aggregate difference which does not exceed two times this average deviation (a.d.) divided by the square root of the number (n) of the trees used in the test."

Algebraically this may be written as follows: Aggregate difference of test sample should be equal to or less than $\frac{2(\text{a.d.})}{\sqrt{n}}$ Where a.d. is the average deviation of the table to be tested (for these tables use 4 per cent) and n is the number of trees in the test sample taken in the stand to be estimated.

The method of making the applicability check can best be illustrated by an example.

1. In the black spruce stands to which the tables are to be applied, obtain diameter measurements inside and outside of the bark on not less than 15 trees. The diameter breast high and the total heights of the test trees should cover the range of heights and diameters and also the range of volumes of the trees in the stand. Measure the diameters at the points given under tree measurements on page 3. Record on U. S. D. A. Form 558 when possible.

2. Compute the unpeeled total stem volume in cubic feet, preferably by the planimeter method, or by the conventional formula method.

3. Tabulate the diameter breast high (D.B.H.), total height, and actual tree volume as shown in Table VII.

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[5] Committee Report. Method of preparing volume and yield tables. Jour. For. 24, pp. 653-666. 1926.

TABLE VII

Test Sample Illustrating Method of Making Applicability Check

Tree No.	D.B.H.	Total height	Unpeeled total volume		Difference
			Actual	Tabular	
	in.	ft.	Cubic feet		Cubic feet
1	9.3	63	15.6	15.2	0.4
2	6.5	58	6.8	7.2	0.4
3	7.3	62	9.6	9.5	0.1
4	8.6	56	12.0	11.8	0.2
5	5.9	54	5.5	5.6	0.1
6	6.3	56	6.9	6.6	0.3
7	4.0	42	2.0	2.1	0.1
8	7.8	54	9.5	9.4	0.1
9	7.0	58	8.0	8.2	0.8
10	6.6	52	6.6	6.7	0.1
11	8.9	63	13.7	13.9	0.2
12	8.6	66	14.0	13.5	0.5
13	4.7	52	3.7	3.6	0.1
14	8.1	58	10.7	10.7	0.0
15	7.2	60	8.8	9.0	0.2
16	5.5	52	5.1	4.8	0.3
Total	...	...	138.5	137.8	3.9

$$\text{Aggregate difference} = 100\ \frac{(138.5-137.8)}{137.8} = 0.5 \text{ per cent.}$$

$$\text{Average deviation} = 100\ \frac{(3.9)}{137.8} = 3 \text{ per cent.}$$

4. For each tree in the test sample, determine the tabular volume (unpeeled total stem volume) corresponding to the actual diameter, to the nearest tenth of an inch, and the actual height to the nearest foot. This can most easily be done by using the volume table in alinement form, Figure 1. The volume of a tree of given diameter and height can be read very easily by placing a transparent straight edge across the axes as illustrated by the dotted line, i.e., the unpeeled total stem volume of a tree 9.3 inches in diameter breast high and 63 feet in height is 15.2 cubic feet as read from the volume axis.

5. Compute the aggregate difference of the trees in the test sample as follows: Take the difference between the sum of the tree volumes and the sum of the tabular volumes and express this as a percentage of the sum of the table volumes. This aggregate difference or percentage of error should be less than the value determined by the formula $\frac{(2)\,(\text{a.d.})}{\sqrt{n}}$. In the assumed test sam-

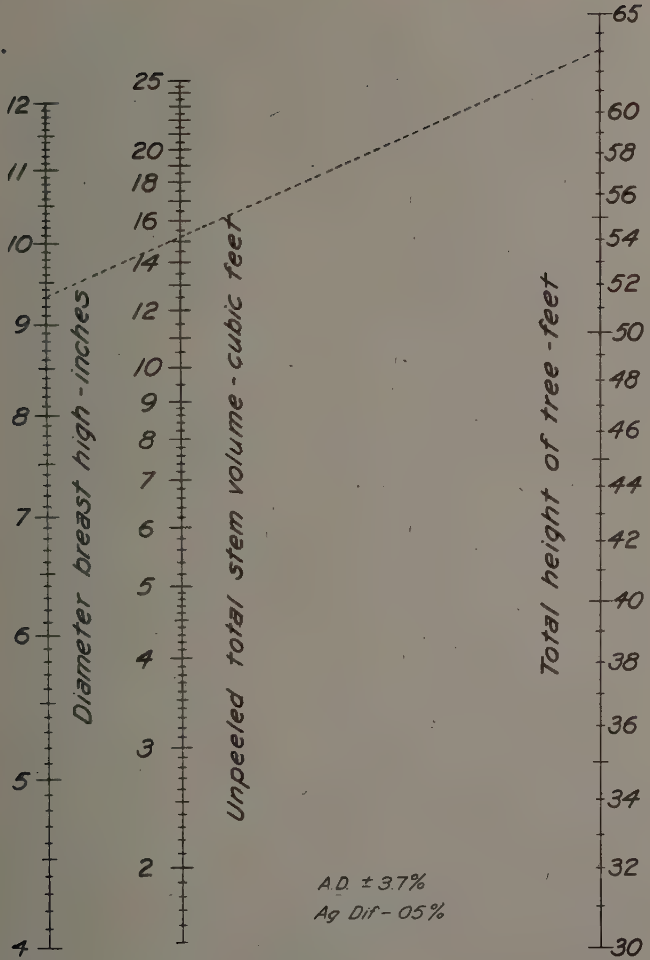

Fig. 1. Alinement Chart Volume Table. Unpeeled Total Stem Volume—Cubic Feet

The dotted line illustrates the method of reading the volume for a given D.B.H. and height.

ple the total volume of the sixteen trees is 138.5 cubic feet and the total of the corresponding volumes read from the chart is 137.8 cubic feet. The volume table therefore underscales the actual tree volumes by 0.5 per cent of the sum of the table volumes. The aggregate difference of the test sample is therefore 0.5 per cent and in this case is less than the value (2 per cent) obtained from the formula $\frac{2 \times 4}{\sqrt{16}}$.

When checking these tables use the formula $\frac{8}{\sqrt{n}}$

6. Compute the average deviation of the volumes of the trees in the test sample as follows: Take the difference between each actual and each tabular volume as shown in the last column in Table VII. Total these differences, regardless of sign, and express this total as a percentage of the sum of the table volumes. This is the average deviation in per cent which should be approximately equal to or less than the average deviation (4 per cent) of the table for a satisfactory check. The average deviation of the test sample, taken as an illustration, is computed by expressing the sum (3.9 cubic feet) of the differences as a percentage of 137.8 cubic feet. This is an average deviation of 3 per cent, which is less than the average deviation of the volume table.

The applicability check of the assumed test sample shows that the volume table scales the volumes of the trees in the sample within the accepted limits of error. The average deviation of the sample was also found to agree with that of the table. One would conclude, therefore, that these tables are suitable with out correction for estimating the stand of black spruce from which the assumed sample was taken without introducing an error due to the inapplicability of the volume tables.

METHOD OF CORRECTING THE TABLE IF THE VARIATION EXCEEDS THE ACCEPTED LIMITS[6]

If the applicability check shows that the average deviation and aggregate difference in per cent exceed the accepted limits, the tables may be corrected as follows: Group the tabular volumes in one-foot volume classes, i.e., all trees having a table volume from 0 to 1.9 are placed in the one-foot volume class; those from 2.0 to 2.9 are placed in the two-foot volume class, etc. For each class compute the average tabular volume and the average of the corresponding test-tree volumes. When a sample containing 15 trees is used, grouping is not necessary. On logarithmic cross-section paper plot the average actual tree volumes over the corresponding average table volumes. (Fig. 2.) Balance a curve or straight line[7] in among these averages, and from this curve read the corrected volume for each volume found in the uncorrected table. For example, the corrected volume for a 6-inch 50-foot tree would be read from the above curve over a table volume on the horizontal axes of 5.4 cubic feet, i.e., the volume of a tree of that size found in Table III. (See dotted line in Fig. 2.)

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[6] This procedure is a step in the alinement chart method of making volume tables.

The corrected peeled total and merchantable volume tables can be obtained from the uncorrected unpeeled total stem volume table by a similar procedure. Compute the peeled total stem and merchantable volumes for each tree in the test sample. By a procedure similar to that above classify, average, plot, and curve each series of volumes on the basis of the uncorrected unpeeled total stem volume. To insure consistent results between inside and outside bark volumes and between total and merchantable volumes these curves should be compared with each other by percentages. From this series of curves, read the corrected peeled total and merchantable volumes. The corrected volume table in cords can be obtained by dividing the corrected unpeeled merchantable volumes in cubic feet by the converting factors given in the uncorrected table.

Merchantable Limits

When the merchantable volume tables are used in estimating, allowances should be made if the top cutting limits in the table do not agree with the limits to which the trees will be cut.

Deductions for Defect

No deductions for defect have been made in these tables. In applying them, deductions should be made to obtain the net volume.

Volume of a Single Tree

The average volumes given in a volume table represent a series of volumes that differ one from another. These differences are compensating only when a table is applied to a relatively large

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[7] A straight line through the origin (1.1) at 45 degrees indicates that no correction is necessary.

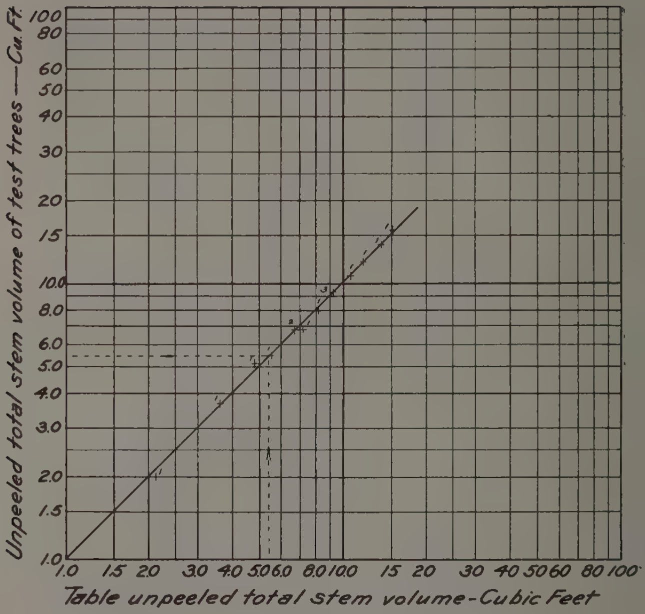

Fig. 2. Method of Adjusting Volumes in Tables by Means of Volumes of Test Trees

The dotted line illustrates the method of reading the corrected volume for a 6-inch 50-foot tree. (The closeness with which the line approaches a 45-degree line through the origin shows that a correction is not necessary in the example cited.)

number of trees in a stand to which the table is applicable. The average deviation indicates that the volume of a single tree, taken at random in a stand to which the tables are applicable, may differ, on the average, from the table volumes by 4 per cent. In some instances the volume of a single tree may vary from the table volumes by as much as 15 per cent. For these reasons, the volume of a single tree can not be accurately determined by these volume tables.

If the above precautions are taken and the tables are checked and adjusted when necessary they can be used to estimate black spruce stands under any conditions.

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POTATO BREEDING METHODS II
SELECTION IN INBRED LINES[1]

F. A. KRANTZ AND A. E. HUTCHINS

INTRODUCTION

The amount of potato breeding work in progress in America is much less than that of other important food crops. This neglect exists in spite of serious defects in the important commercial potato varieties. The early types will illustrate this condition. Bliss Triumph, owing to its red tuber color and its limited climatic adaptability, is restricted in production to special regions and in consumption to certain markets. Furthermore, great difficulty is experienced in maintaining seed stocks of this variety free from virus diseases. Irish Cobbler has deep eyes with a consequent inconvenience in peeling and waste in utilization; a condition that is a trial to the housewife and should not exist. Early Ohio has a tendency to form knobs and growth cracks when growing conditions vary slightly throughout the season. This frequently results in serious economic losses to the growers. The American grower who desires to produce early potatoes, or who finds quick maturing varieties more desirable for his conditions, is limited to a choice of these three varieties.

Two late maturing varieties, Green Mountain and Rural New Yorker No. 2 and their prototypes, comprise the bulk of the main crop in the United States. They are the best adapted to Minnesota of the late maturing sorts. This fact is attested to by the results of tests in different parts of the state in the last fifteen years, and also by the fact that they have displaced the other late maturing types. These late varieties, however, are not adapted to some of the important potato growing regions of Minnesota, and most of the growers in these regions, particularly in the Red River Valley, are using one of the early varieties for their main crop.

Another indication of the lack of adaptability is the low average yields obtained in comparison with those in other regions in the United States. These low yields are not due to lower soil fertility or to less efficient methods of production. They are due to climatic limitations. The growers have partly offset these low yields by increased efficiency in methods of production, until the cost of production per bushel is lower in Minnesota than in other states. The cost of production per acre would not be materially increased by growing an adapted type whose yield would be comparable to that in other regions of the country.

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[1] The potato breeding work here reported was conducted at University Farm, St. Paul, and the Northeast Experiment Station, Duluth, Minnesota. The writers wish to express their appreciation to Superintendent M. J. Thompson of the Northeast station for aid and cooperation during the progress of the work.

The varieties now grown in Minnesota originated in the eastern part of the United States and were probably selected from among other seedlings because of their greater productivity in that region. It is not surprising that productivity was reduced when they were grown under other environmental conditions. No systematic attempt has been made to produce higher yielding commercial types, altho such improvement seems to be possible. In 1921 work was started to produce a higher yielding commercial variety by applying the principle of "selection in self-fertilized lines" to a vegetatively propagated crop. During the progress of this work approximately 40,000 seedlings have been grown. In the experiments reported here only a small proportion of these have been directly utilized. The material used in the experiments was from various sources and was selected with reference to its suitability to the particular experiment. Indirectly, the entire 40,000 seedlings have contributed to the results reported, as it has been possible to select material adapted for the different studies.

The potato is normally self-pollinated. However, as the varieties are vegetatively propagated by tubers and not by seed, they are in a heterozygous condition similar to that obtained in a normally cross-pollinated crop. Consequently the principle of selection in self-fertilized lines that is applied to normally cross-pollinated crops should also be applicable to the improvement of this crop. This method, in brief, is to inbreed continuously until individuals are secured that breed true for their important characters. This process involves the selection of the best individuals in each generation. These are used as parents for the succeeding generation. When individuals of the desired type that breed true are secured, they are recombined in order to restore hybrid vigor, and from the best recombinations the desired commercial variety is selected. As potato varieties are vegetatively propagated, the characters will remain constant thereafter. It will be noted from this brief outline of the procedure that the problem of potato improvement is essentially one of developing superior individuals for breeding purposes. The usefulness of these individuals will not depend upon their own performance but upon their breeding value as ascertained by a study of their progeny; and upon their ability, when crossed, to produce other individuals of economic value.

The necessity of obtaining such individuals for breeding purposes is due to the character of potato varieties. They are extremely heterozygous and often contain recessive factors for undesirable characters. Furthermore, they frequently exhibit a high degree of sterility, and under certain conditions many varieties have a strong tendency to drop their flowers. Selection in self-fertilized lines offers the best means of eliminating these undesirable features. Furthermore, the potato has characteristics that make it particularly well adapted to this method of breeding. It is normally self-pollinated; artificial crosses can be made easily and quickly; and a single pollination usually gives numerous seeds. The seed retains its viability under good storage for ten or more years; and, finally, clonal propagation of individuals may be continued indefinitely.

NON-FRUITFULNESS IN RELATION TO BREEDING METHODS

A potato plant may be non-fruitful for two reasons: (1) Flowers may drop because of the abscission of the flower pedicel; (2) pollen abortion may be great enough to preclude fertilization. There appears to be no direct causal relationship between the two phenomena. Flowers may drop at any state of development, depending upon the variety and the environment under which it is grown. The difference between varieties in the tendency to drop their flowers has been utilized in varietal classification (Stuart, 14). A large group of seedlings or varieties will usually exhibit a continuous gradation, from individuals that drop their buds at a very early stage to those in which apparently no abscission occurs and in which, if the pollen is aborted, the flowers will adhere to the plant until completely desiccated. The latter extreme is not of common occurrence, for the flowers that persist until fully developed, if not fertilized, will usually fall before drying up. Fertilization usually inhibits any further tendency of the flower to drop. Consequently, an indirect relationship exists between pollen fertility of individuals and the abscission of fully developed flowers.

As previously stated, the character of flower abscission is influenced to a considerable degree by environment. At University Farm, flower abscission is sufficiently prevalent to create a serious problem. In spite of the handicap during the four years, 1921-24, distinct progress was made in obtaining seedlings that would flower at University Farm. Since 1924, the seedlings have been transferred after their first year to the Northeast Experiment Station, at Duluth, to obtain an environment where flower abscission rarely occurs. Under average growing conditions at Duluth, seed is obtained from pollen fertile individuals. The elimination of one of the factors responsible for non-fruitfulness has enabled more rapid progress to be made in overcoming pollen sterility.

The potato is normally self-pollinated, consequently inbreeding would be an easy process if it were not for the high degree of pollen sterility in most varieties. The severity and occurrence of pollen abortion in the cultivated varieties have been ascertained by Stout and Clark (12). Their results show that the major economic varieties approach almost complete pollen sterility. In Minnesota there are six important commercial varieties—Early Ohio, Irish Cobbler, Bliss Triumph, Green Mountain, Rural New Yorker, and Russet Burbank. Two others, Burbank and Spaulding Rose No. 4, are occasionally grown. Green Mountain and Irish Cobbler produce a certain amount of seed under proper environmental conditions. Seed has also been secured from Early Ohio and Triumph, tho seed setting in these two varieties is extremely rare. The other four varieties do not set seed in Minnesota.

The progeny of parents that are scant seed setters usually contain a high percentage of non-seed-producing individuals. Fertile seedlings, however, usually can be obtained in all families if a sufficient number are grown. In certain families the number may be so large that the expense involved would not warrant a continuance of the line. As an instance of this, of 882 seedlings of Irish Cobbler grown in 1925, none set seed. They were replanted from tubers the following year and only 5 produced seed. In the third year, 280 of the original seedlings were again planted but seed was secured from only 8 more, thus making possible selection from only 13 individuals, altho many were grown for three consecutive years. The low percentage of seed production in such families decidedly restricts the amount of selection that can be practiced. Seedlings that do not produce seed in the first three years of their existence are generally discarded for breeding purposes, unless they have other special characteristics of value. Some discarded seedlings might set seed if subjected to a wide range of growing conditions, but the possible results would hardly justify the expense involved.

In order to eliminate the necessity of growing such large numbers and to make possible the use of certain poor seed-producing but otherwise desirable parents, such varieties were crossed with seedlings that set seed liberally. The F_1 from these crosses usually contained enough fertile seedlings for inbreeding purposes. There may be extreme cases of sterility in which a second cross of the F_1 individuals with a seed-bearing parent would be desirable.

Many investigators have studied the nature and cause of sterility in the potato. As the results of their work suggest the possibility of mitigating or circumventing the difficulties that arise through sterility, it may be well to discuss them briefly at this point. The number of chromosomes in the potato has been found by Smith (11), Vilmorin and Simonet (15), Stow (13), and Salaman (9) to be 24. Smith (11) concludes that tetraploidy occurs in the Early Ohio, Early Rose, and

Russet Rural varieties. He suggests that if certain varieties are triploid, as seems to be the case from Lutman's (4) study of Irish Cobbler, Green Mountain, Lookout Mountain, and Early Rose, this might at least partially explain pollen sterility. Stow (13) noted abnormal division of the pollen mother cells, and showed that there was a varietal difference in this respect. He believes "that the abnormal division is neither connected with the hybrid nature of the plant nor the nutritive correlation within its body; but rather due to the environmental conditions or certain special nature of the plant itself." He considers that sterility is mainly the result of abnormal pollen mother cells, which he observed at high temperatures (25° 35°C.). "At lower temperatures (15°-20°C.) on the other hand, the reduction proceeded in a regular manner, producing normal pollen grains." If this interpretation is correct, it may be possible to obtain seed from sterile varieties by experimentally subjecting them to the proper temperatures. This would materially facilitate potato breeding work.

The fact that certain pollen grains abort while others in the same individual survive and are capable of functioning leads to the assumption that pollen grains are differently constituted. This assumption is further supported by results obtained by Salaman and Lesley (10), who have shown by reciprocal crosses that the greater portion, if not all, of the sterility is inherited through the egg. The fact that the eggs will survive conditions that prove lethal to the pollen grains may account to some extent for the widespread prevalence of sterility in cultivated varieties. By the process of inbreeding, sterility would be eliminated through the aborted pollen, and that which was carried over in the egg would be further reduced by elimination of the non-fruiting individuals. These theoretical considerations receive experimental verification from the results of inbreeding. There is a noticeable increase in the number of fertile individuals after the second inbred generation, and lines have been isolated in the third and fourth generations in which a high percentage of individuals are fruitful.

Pollen sterility in the potato makes selection in inbred lines a laborious process. Selection is necessarily restricted to the seed-bearing individuals, and the number of these is frequently limited in the early generations. This necessitates the growing of large populations, only part of which can be utilized. As inbreeding continues, the relative number of fertile individuals increases. Coincidentally other characters have also tended to become homozygous. Consequently the material is less suitable for the selection of the particular combinations desired. This difficulty can be overcome to some extent by crossing desirable sterile types with the best highly fertile types, following by inbreeding and selection in the progeny.

GENERAL EFFECT OF INBREEDING ON THE POTATO

The general effect of inbreeding on the potato is at first to expose to view the heterozygous condition of a potato variety. The variability in the first-generation progeny is very marked. A variety will usually segregate for the easily observable characters that are commonly associated with the individuality of a variety. The variability of this progeny is further emphasized by the appearance of recessive characters. In the second generation some of the lines breed true for certain characters and begin to show individuality. The differentiation into more stable breeding lines is noticeable in the third generation, in which some of the lines assume a distinctive identity while others may still be segregating for important characters.

YIELD OF INBRED LINES

As the lines increase in homozygosity, in general, a loss in vigor occurs. In Tables I and II the relative amount of vine growth and the yields of different inbred generations of two varieties are given. In Table I it will be noticed that the yield is distinctly lower in the second generation than in the first in both 1923 and 1927, when comparative yield tests were made. The yields of the later generations, in which all the lines of each generation are grouped, do not show a significant further decrease.

TABLE I

YIELD OF INBRED LINES DERIVED FROM MINNESOTA ACC. NO. 7416

Year	Generation	No. of lines	Vine growth*	Av. yield, lb.
1923	1	1	4.8	0.39
1923	2	11	4.5	0.28
1925	2	7	4.8	0.35
1925	3	2	4.4	0.38
1927	1	1	3.5	0.84
1927	2	4	2.6	0.42
1927	3	8	4.0	0.43
1927	4	11	3.4	0.31
1928	2	2	6.0	1.49
1928	3	5	6.7	1.07
1928	4	3	6.3	1.76
1928	5	7	6.5	0.84

* Average rating of individuals on a scale of 10.

In Table II the inbred generations of the Early Ohio are compared. The comparative yields obtained in 1927 and in 1928 suggest that very little loss, if any, occurred in this stock after four generations of inbreeding. The yields given in the effect of inbreeding are based on yield of seedlings that survive through the first season. There is frequently a high mortality. The more vigorous seedlings are probably the ones that survive. This tends to raise the average yield of the weaker lines. Furthermore, the vigorous seedlings are more likely to flower and set seed and consequently become the parents of succeeding generations.

TABLE II

Yield of Inbred Lines Derived from Early Ohio

Year	Generation	No. of lines	Vine growth	Av. yield, lb.
1927	1	1	4.6	0.82
1927	2	2	4.3	0.62
1927	3	18	5.3	1.03
1928	2	5	8.5	1.86
1928	3	4	8.5	1.88
1928	4	16	6.8	1.37

Data presented in Table III illustrate this condition to some extent. The decline in vigor was different in the four lines derived from the same variety. A more rapid decline in vigor occurred in strains B, C, and D, than in strain A. The table further shows that strain A was easier to maintain than the other three strains. Strains B, C, and D, after the initial decline in yield in the second generation, showed no distinct further drop. Strain A gradually declined in yield and by the fourth generation its yield was approximately the same as that of the other strains.

TABLE III

Yield and Vine Growth of Four Inbred Strains of Minn. Acc. No. 7416 Self-Fertilized fof Four Generations

Year	Inbred Generations	Strain A		Strain B		Strain C		Strain D	
		Vine	Yield	Vine	Yield	Vine	Yield	Vine	Yield
			lb.		lb.		lb.		lb.
1923	1	4.8	0.39	4.8	0.39	4.8	0.39	4.8	0.39
1923	2	5.8	0.50	4.9	0.32	3.5	0.27	5.2	0.30
1925	2	6.5	0.58	5.3	0.40	...	....	...	....
1925	3	4.6	0.46	...	....	...	....	4.2	0.30
1927	1	3.5	0.84	3.5	0.84	3.5	0.84	3.5	0.84
1927	3	4.2	0.63	...	....	2.5	0.26	2.5	0.28
1927	4	3.4	0.31	3.4	0.31	...	....	...	....

The data presented on the effect of inbreeding on vigor show that there is a general tendency for vigor to be reduced by inbreeding. Owing to elimination of weak seedlings and of lines through failure to set seed, the actual reduction is probably more than the figures indicate. The amount of vigor lost is not so large but that the more vigorous lines can be maintained and utilized.

YIELD OF CROSSES

A study was made to determine the effect of crossing on vigor in the potato, in order to ascertain whether the loss of vigor which accompanies inbreeding could be regained when the best inbred selections were recombined. The method of testing the different combinations varied considerably, depending on the amount of material available. The individual plots usually consisted of 50 seedlings, altho frequently a much higher number was used. The number of plots varied from four systematically distributed plots to single ones.

In Table IV, a comparison is given of the vine growth and yield of fifteen crosses together with that of the progenies of parental varieties. In ten of the eleven crosses for which yield data are available for each parent and the F_1 progeny, the cross-bred individuals gave a higher yield than the mean yield of the two parents. The highest percentage increase obtained over the mean of the parents was 125.7. One F_1 family gave a lower yield than the mean yield of the two parents. If the F_1 progenies are compared with the higher yielding parents in each case, they still show an increase in all but one cross. In this relation the highest percentage increase was 89.2. In this particular cross, two individuals that gave low-yielding progenies produced a relatively high yielding F_1 progeny. An average of the eleven F_1 progenies shows that they outyielded the average mean of the parents by 50.3 per cent, and the average yield of the highest yielding parent by 31.5 per cent.

The differences obtained between the yield of F_1 crosses and that of the progenies of their parents were larger than those obtained between the different inbred generations. This difference in yield may be due to a combination of loss in vigor from selfing the parents and an increase in vigor due to crossing. The yields of three parental families and of their F_1 progenies were compared. This tends to eliminate any decrease in yield that may have occurred because of selfing the parents. The results seem to indicate that the greater part of the difference is due to the beneficial effect of crossing rather than to any detrimental effect of inbreeding.

The data presented in Table V show a decided increase in yield from crossing in two cases and practically no gain in the other case.

The general tendency of the F_1 progenies to be vigorous and high yielding has an important bearing on breeding methods. The data given in Tables IV and V show that progenies derived from either seedlings or varieties are distinctly inferior in yielding ability to the F_1 progenies. In fact, no seed has been obtained from any source that gives progeny yielding as high as the progeny of crossed seed. In observations made on approximately thirty thousand seedlings, few

TABLE IV

Comparison of F_1 Crosses with Progenies of Parental Varieties

Year	Cross	Vine growth			Average yield lb.			Inc. in yield over mean of parents per cent	Inc. in yield over highest parent per cent
		♀	♂	F_1	♀	♂	F_1		
1923	Green Mountain × Minn. Acc. No. 7416	5.9	4.8	6.5	0.27	0.39	0.61	84.8	56.4
1923	Irish Cobbler × Lookout Mountain	5.6	5.4	6.1	0.28	0.26	0.53	96.2	89.2
1923	Early Ohio × Minn. Acc. No. 7416	5.8	4.8	5.8	0.49	0.39	0.51	15.9	4.0
1924	Triumph × Minn. Acc. No. 7416	4.0	5.1	5.3	....	....	....	....	....
1924	Irish Cobbler × Minn. Acc. No. 7416	4.6	5.1	4.8	....	....	....	....	....
1925	Irish Cobbler × Peerless	5.0	6.1	5.9	0.37	0.32	0.49	42.0	32.4
1925	Irish Cobbler × Minn. Acc. No 7416	5.0	...	4.6	0.37	....	0.39	....	5.4
1925	Peerless × Lookout Mountain	6.1	...	6.2	0.32	....	0.42	....	31.2
1925	41.22-40-24 × 28.22-8-24	5.5	4.6	6.7	0.36	0.46	0.55	34.1	10.5
1927	Triumph × 12.23-4.1-25	2.5	3.0	3.8	0.65	0.39	0.76	46.1	16.9
1927	Cobbler × 12.23-4.2-25	4.4	3.0	4.3	1.03	0.39	0.61	—16.3	—68.8
1927	Triumph × 41.22-2-25	2.5	4.0	4.1	0.65	0.88	1.17	52.0	32.0
1927	15.22- 1-25 × 41.22-2-25	2.0	4.0	4.0	0.20	0.88	1.15	112.9	30.6
1927	15.22- 1.25 × 4.20-10.4-25	2.0	3.0	4.0	0.20	0.66	0.69	60.4	4.5
1927	12.23-10.25 × 4.20-10.4-25	3.0	3.0	4.6	0.39	0.66	1.21	125.7	83.8
							Average	50.3	31.5

progenies have been found to approach the vigor of crossed seed and none that equaled the vigor of the heaviest yielding F_1 progenies. Consequently it should be far easier to select seedlings from the F_1 progenies that would be higher yielding than the commonly grown varieties than from progenies of any other source.

TABLE V

YIELD OF THE P_1 GENERATION COMPARED WITH THE F_1

Year	Parental families ♀ P_1	Parental families ♂ P_1	Vine growth ♀ P_1	Vine growth ♂ P_1	Vine growth F_1	Average yield, lb. ♀ P_1	Average yield, lb. ♂ P_1	Average yield, lb. F_1	Inc. yield over mean of parental families per cent	Inc. yield over highest parental family per cent
1927	42.44 ×	15.22	4.36	2.00	3.74	1.026	0.200	0.63	3.2	—63.4
1927	15.22 ×	4.20	2.00	3.48	4.64	0.200	0.844	1.24	138.4	47.6
1927	41.22 ×	4.20	4.58	3.48	5.60	0.819	0.844	1.42	71.0	69.0

Studies on the vigor and yielding ability of F_2 and later generations show that vigor and yield tend to decline after the F_1 generation. The comparative yield and vine growth for F_1 to F_3 generations of two crosses are given in Table VI. A small reduction in yield occurred in the F_2 generation and a greater in the F_3 generation. In this limited study the decline was greater in the F_3 generation than in the F_2 or the F_4 generation.

TABLE VI

RELATIVE VIGOR OF F_1 TO F_3 GENERATIONS OF TWO CROSSES

Cross	Year	Generation	No. of lines	Vine growth	Av. yield per seedling lb.
13.22-18-24 × 28.22-8.24	1927	F_1		6.5*	1.14*
	1927	F_2	5	7.6	1.22
	1927	F_3	2	6.3	0.93
41.22-40.24 × 28.22-8.24	1927	F_1		6.7*	1.10*
	1927	F_2	2	6.4	0.97
	1927	F_3	34	4.9	0.77
	1928	F_3	4	7.5	1.99
	1928	F_4	13	6.9	2.27

* Adjusted on the basis of checks from 1926 data.

The data presented on the effect of inbreeding and cross-breeding indicate a general tendency for vigor to be reduced through inbreeding. This loss is probably greater than the yield data indicate, because of the loss of weak seedlings and the tendency to eliminate weak seedlings and lines through their failure to set seed. Cross-breeding has a tendency to increase the vigor, as is shown by the greater vigor in the F_1 progenies. One may assume, therefore, that crossing desirable inbred lines results in vigor equaling or surpassing that of the original parents.

Selection in Inbred Lines

The physical limitations on the number of lines that can be grown makes it obligatory to practice some type of selection so the desirable germ plasm can be sorted out and saved and the undesirable discarded. Most of the desirable morphological characters have been segregated by selecting individuals possessing them and by testing the correctness of the observations through a study of the progeny in later generations. The isolation of these characters appears to be progressing so well that no special studies have been deemed necessary to determine a more accurate basis for the selection. Some of the plant characters isolated on the basis of field records and observations are differences in color and form, second growth, growth cracks, depth of eye, smoothness and russeting of tubers, length of stolons, number of stolons, number of tubers per stolon, number and size of tubers per plant, habits of vine growth, and other vine characters. Two other characters, yield and time of maturity, were studied to determine on what basis selection for them could be made most effectively.

BREEDING BEHAVIOR OF EARLY AND LATE VARIETIES

To determine the relationship between the time of maturity of plants and the breeding behavior of their progeny, a study was made of the progenies of commercial varieties whose relative time of maturity is well known. These varieties fall naturally into two classes.

Early maturing	Bliss Triumph Irish Cobbler Early Ohio
Late maturing	Green Mountain Rural (smooth and russet) Red McCormick (Lookout Mountain)

Altho the varieties within these groups vary, the groups are fairly well defined. As the phenotypic behavior has been well established by observations of commercial plantings throughout the country, a study of their genotypes should be of interest. The breeding behavior of these varieties was determined from a study of their progeny and from the progeny derived from crosses in which they appear as parents.

By reference to Table VII it may be seen that the maturity of the seedlings corresponded rather closely to that of the parents. In 1923, the progenies of Early Ohio and Lookout Mountain were compared. The Early Ohio had matured 54 per cent of its progeny on September 10; the Lookout Mountain, 8 per cent. In 1924 a study was made of the progenies of the Triumph and Cobbler varieties. The Triumph had matured 77 per cent of its seedlings by September 10; the Cobbler, 54 per cent. In 1927 a comparison was made of the relative time of maturity of the progeny of Triumph, Cobbler, Early Ohio, and Green Mountain. The percentage matured by September 10 in the four varieties was 73, 63, 50, and 10, respectively. On the basis of time of maturity of offspring, the five varieties may now be listed in the following order: Bliss Triumph, Irish Cobbler, Early Ohio, Green Mountain, and Red McCormick.

TABLE VII

BREEDING BEHAVIOR OF FIVE COMMERCIAL VARIETIES AS INDICATED BY THE COMPARISON OF THEIR SEEDLING PROGENY IN RELATION TO THE NORMAL PERIOD OF MATURITY

Variety	Year	Condition of seedlings on September 10			
		Number			Percentage mature
		Mature	Immature	Total	
Early Ohio	1923	120	101	221	54
Red McCormick	1923	3	34	37	8
Triumph	1924	108	32	140	77
Cobbler	1924	6	5	11	54
Triumph	1927	63	23	86	73
Cobbler	1927	26	15	41	63
Early Ohio	1927	13	13	26	50
Green Mountain	1927	5	47	52	10

A comparison of the behavior of the varieties in crosses with a common pollen parent further confirms the results from the study of progenies obtained by self-pollination. Six groups of such crosses are shown in Table VIII. Triumph, Cobbler, and Early Ohio retain their relative ranking when crossed with a medium early parent, Minn. Acc. No. 7416. The percentage of F_1 progeny mature on September 10, 1923, was 86, 77, and 50, respectively. A similar test of Triumph and Cobbler in 1924 gave respectively 62 and 52 per cent of mature seedlings on September 10. In the four succeeding groups of crosses, the progeny of Russet Rural is compared with that of Triumph, Cobbler, and Green Mountain. In Group III, Triumph and Russet Rural are crossed with a very late maturing parent, 4.20-1-24. The percentage of the F_1 progenies mature on September 10, was 24 and 19, respectively. When these varieties were crossed with a medium late maturing seedling, 41.22-1-25, the F_1 progenies matured 35 and 6 per cent of their respective seedlings by September 10. In Group V, Cobbler and Russet Rural are crossed with a late maturing seedling, 11.24-1-25. In the F_1 progenies of these crosses the percentage of mature seedlings was 39 and 20, respectively. In Group VI, where two late varieties, Green Mountain and Russett Rural, were crossed with a late maturing seedling, 11.24-3-25, the F_1 progeny of the Russet Rural cross matured 9 per cent more of its seedlings by September 10 than did the progeny of the Green Mountain cross. The results of these crosses tend to confirm the previous ranking of Triumph, Cobbler, Early Ohio, and Green Mountain based on the behavior of progeny of self-pollinated seed. Russet Rural appears from the data obtained in these crosses to be genetically slightly earlier than Green Mountain.

From the data presented in Tables VII and VIII, some general deductions seem to be justified. The early maturing varieties –Triumph, Cobbler, and Early Ohio—give distinctly earlier maturing progeny than the late varieties—Rural, Green Mountain, and Red McCormick. The difference between the time of maturity of the seedling progeny of the early maturing varieties is greater than between the individual varieties when these varieties are asexually propagated. The value of a seedling or a variety in respect to the character of maturity can be more quickly and accurately ascertained by studying its breeding behavior in comparative tests than from its phenotypic behavior.

TABLE VIII

Factors for Maturity of Six Commercial Varieties as Indicated by Their Behavior in Crosses

Group	Parents	Year	Condition of seedlings on September 10			
			No. of seedlings			Percentage mature
			Mature	Immature	Total	
I	Triumph × Minn. Acc. 7416	1923	42	7	49	86
	Cobbler × Minn. Acc. 7416	1923	40	12	52	77
	Early Ohio × Minn. Acc. 7416	1923	30	30	60	50
II	Triumph × Minn. Acc. 7416	1924	54	33	87	62
	Cobbler × Minn. Acc. 7416	1924	43	39	82	52
III	Triumph × 4.20-1-24	1927	22	70	92	24
	Russet Rural × 4.20-1-24	1927	7	29	36	19
IV	Triumph × 41.22-1-25	1927	11	20	31	35
	Russet Rural × 41.22-1-25	1927	2	29	31	6
V	Cobbler × 11.24-4-25	1927	12	19	31	39
	Russet Rural × 11.24-4-25	1927	7	28	35	20
VI	Green Mountain × 11.24-3-25	1927	6	27	33	18
	Russet Rural × 11.24-3-25	1927	9	24	33	27

INHERITANCE OF TIME OF MATURITY

An analysis of the data on a strict genetic basis can not be made. The data are, however, suggestive of several points. Müller (5) studied the genetic characteristics of potato varieties of different maturity. His results show that the later the average maturity the greater is the negative skewness of the frequency curve; the earlier the average maturity of a family the greater is the variability as measured by the standard deviation; the means of the crosses lie between the means of the progeny of the self-pollinated parents. Müller attempts to explain these results on the basis that late maturity is dominant and that multiple factors are involved. He points out that the increased variability of the early families does not harmonize with the supposition that late maturity is dominant. He suggests that this discrepancy might be accounted for by the shorter period of daylight and dropping of temperature as the season progresses, thus prolonging the life of individuals and placing them in later classes than their genotype would warrant. It appears, however, that the results could be more easily explained if it were assumed that earliness was dominant and that multiple factors were involved. Müller was working with medium early varieties that would probably be heterozygous for this character. This would account for their greater variability as compared to the progenies of the late maturing varieties; the latter, having more homozygous recessive factors, would tend to breed true.

TABLE IX

COMPARISON OF TIME OF MATURITY OF PROGENY OF COMMERCIAL VARIETIES AND THEIR F_1 VARIETAL CROSSES

No.	Parents	Maturity of parents	Year	Condition of seedlings on September 10			
				Number of seedlings			Percentage mature
				Mature	Immature	Total	
I	Triumph	Early	1924	108	32	140	77
	Triumph × Minn. Acc. No. 7416			54	33	87	62
	Minn. Acc. No. 7416	Medium		15	56	71	21
II	Cobbler	Early	1924	6	5	11	54
	Cobbler × Minn. Acc. No. 7416			43	39	82	52
	Minn. Acc. No. 7416	Medium		15	56	71	21
III	Early Ohio	Early	1923	120	101	221	54
	Early Ohio × Minn. Acc. No. 7416			30	30	60	50
	Minn. Acc. No. 7416	Medium		17	22	39	44
IV	Triumph	Early	1927	63	23	86	73
	Triumph × 41.22-2-25			12	5	17	71
	41.22-2-25	Late		7	13	20	35
V	Cobbler	Early	1923	6	2	8	63
	Cobbler × Red McCormick			36	27	63	57
	Red McCormick	Late		3	34	37	8
VI	Triumph	Early	1927	63	23	86	73
	Triumph × No. 12.23			30	39	69	43
	No. 12.23	Late		33	59	92	36
VII	Green Mountain	Late	1927	5	47	52	10
	Green Mountain × 11.24-3-25			6	27	33	18
	11.24-3-25	Late		..	..	..	..

In studies made at University Farm in which the behavior of crosses was compared with that of seedling progenies of the same parents, earliness tended to behave as a dominant character. The data are presented in Table IX. It will be noted that in crosses I, II, and III, in which the early varieties were crossed with a medium maturing parent, the F_1 seedlings approached more closely in behavior the progeny of the early parent. The data from these three crosses further show a relationship between the earliness of the early parent progeny and of the F_1 seedlings. In crosses IV, V, and VI, early varieties were crossed with late varieties. In two of these crosses, IV and V, earliness behaved as a dominant character; the percentage of seedlings that matured by September 10 nearly equaled the percentage that matured in the progeny of the early parent. In cross VI, the F_1 progeny behaved more like the seedlings of the late parent. In cross VII, in which two late parents were crossed, the F_1 seedlings were late. In the crosses reported by Müller (5) the F_1 progeny clearly tended to be intermediate between the two parents. Since varieties classed as second earliest were used, they were probably later maturing than Bliss Triumph and Irish Cobbler, which would explain the difference in the results obtained.

SELECTION FOR EARLY MATURITY

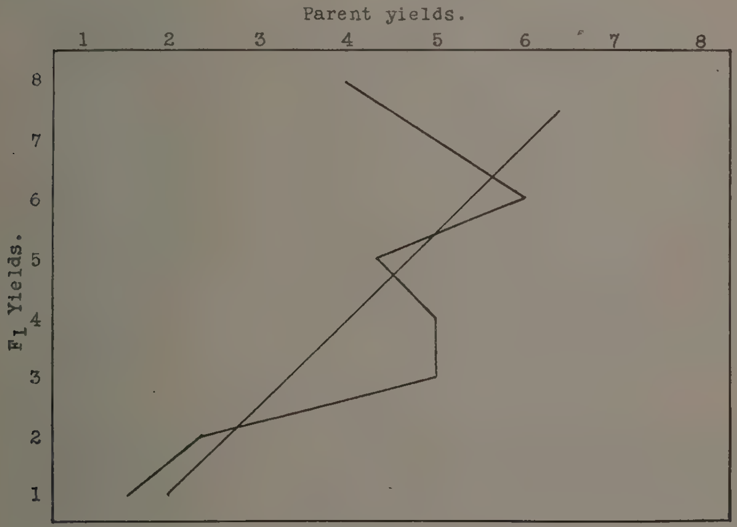
It is interesting to note that the earliest varieties obtainable in the United States, i.e., Bliss Triumph, Irish Cobbler, and Early Ohio, did not breed true for earliness. As these varieties are heterozygous for at least some of the factors that produce earliness, it should be possible to obtain seedlings from their progenies that were more homozygous and consequently earlier maturing than the parent varieties. While selection of the earlier maturing seedlings can be started to advantage in their first and second years, it is not until the third season, because of a tendency to delay maturity, that an accurate comparison with the parent variety can be made. Delayed maturity of the seedlings appears to be associated with the amount of reserve nutrients available when the plants are started. As the size of the tubers available for planting from individual seedlings the second year may vary, some error is involved in making the selections on maturity at this time. A comparison with the parent variety of 229 Irish Cobbler seedlings in their third season indicates that both earlier and later maturing seedlings were obtained. The comparison showed 98 seedlings to be earlier than, 91 similar, and 40 later than the parent. If such progenies were fruitful it would be easy to obtain individuals that would breed true for earliness. But the progenies from early varieties have been highly unfruitful.

In order to obtain early seedlings with viable pollen, crosses of fertile seedlings and early seedlings of varieties were made. This was done because of the difficulty of obtaining early lines from late parents, which, owing to their high fertility, were the best sources of inbred lines. More recently some early lines have been isolated from early varieties. This method of crossing followed by inbreeding, and then repeating the process if necessary, appears to be a satisfactory one for obtaining early seedlings that have viable pollen and the other characteristics desired. A comparison of the progeny of the 34 earliest seedlings with the progeny of Triumph, Cobbler, and Early Ohio shows that 6 seedlings from their breeding behavior appear to be genetically as early as the Triumph variety; 20 seedlings are genetically earlier than the Cobbler or as early; while all of the 34 seedlings are genetically as early as the Early Ohio or earlier. All these seedlings, judging from their ability to set seed, have sufficient viable pollen to function as pollen parents. A comparison, in 1927, of 172 families, including self and F_1 families derived from certain commercial varieties, shows that there were 8 seedling families as early as the Triumph family; 24 families as early as the Cobbler family or earlier; 74 families as early as the Early Ohio family or earlier; 147 families as early as the Green Mountain family or earlier. Twenty families of the 172 in the test were as late as the Red McCormick family or later. The individuals of all the families in the latter class were still green when they were killed by frost, consequently their relative rank could not be ascertained. The number of seedlings of each family is too small to allow a definite conclusion to be drawn as to the relative earliness of any particular family. They show as a group, however, that definite progress is being made toward the production of breeding material that has the combination of earliness and fertility.

The studies on maturity may be briefly summarized. The breeding behavior of standard commercial varieties when self-pollinated and when crossed show that where wide differences in maturity exist a distinct difference will also be found between the genotypes of these varieties or individuals. The Triumph, Cobbler, and Early Ohio varieties, which mature at relatively the same time, show distinct differences in their genetic constitution in regard to maturity. Therefore, in selecting for earliness, late maturing seedlings can be safely discarded, while the early maturing seedlings should be further sorted out on the basis of breeding behavior. The breeding behavior of early maturity as a character appears to be typical of characters whose expression is dependent on dominant multiple factors. The method used to obtain early breeding stock was to cross selected fertile seedlings and early seedlings or varieties, and again select in the inbred lines obtained from the F_1 progeny. This process can be repeated, using the earliest lines obtained, until the lines are as early as the earliest seedlings or varieties obtainable. Seedling lines have been obtained by this method that compare favorably in early maturity with the progeny of the early varieties and, in addition, have the fertility required in breeding stock.

PRODUCTION OF HIGH YIELDING SEEDLINGS

It has been shown in Tables I to VI that there is a tendency for the yield to decrease during the process of inbreeding, and that this loss in yield is regained and frequently increased by appropriate crossing. All crosses do not yield equally well, hence it is important to know what relation, if any, exists between the yields of parents and their corresponding crosses. A few studies have been made of corn, bearing on the relation between the inbred strains and the F_1 crosses. Kisselbach (2) found that high yielding corn strains have, as a rule, given better yielding F_1 crosses than low yielding strains. Richey (7) and Richey and Mayer (8) found no such general relation. More recently Nilsson-Leissner (6) and Jorgenson and Brewbaker (1) obtained results which led them to conclude that selection of the most vigorous selfed lines is desirable in corn, but that the only method of learning the better F_1 combinations is by actual trial.



In 1927, the yields of 47 F_1 potato crosses were obtained. Owing to soil variability at the Northeast station, where all the parents were grown, the yields of these parents were not sufficiently accurate to justify their use. Both parents of 18 of these F_1 crosses were also grown at University Farm. The regression of parent yields on yield of F_1 is shown in Figure 1. The correlation coefficient is 0.5564 ± 0.1079.

This shows a distinct correlation between the mean yield of the parents and their F_1 progeny. The number of crosses involved was small. The parents were very heterogenous as to origin; and it is possible that the high yielding parents were better adapted to growing conditions at University Farm, consequently their F_1 progeny were also better adapted. The results suggest the desirability of further studies to determine if such a general relationship can be expected. Even if such a general relationship exists, there would be little reason for discarding the poorer yielding lines before determining by actual trial their value in recombinations.

A comparison of the yield of F_1 crosses with that of inbred lines and seedling families of standard varieties indicates that a high yield can probably be obtained by recombining the inbred lines even if no selection is made for this character. In 1927, seedling families were grown from Triumph, Cobbler, Early Ohio, and Green Mountain varieties. The lowest yielding family was obtained from the Triumph variety with 52 bushels per acre. The Green Mountain family gave the highest yield, 103 bushels per acre. Of the 57 inbred lines in the test 9, or 15.8 per cent, gave a higher yield than the Green Mountain family, and 25, or 43.9 per cent, gave a lower yield than the Triumph family. Of the 47 F_1 crosses in the test 25, or 53.2 per cent, gave a higher yield than the Green Mountain family and only 3, or 6.4 per cent, gave a lower yield than the Triumph family. It is of interest to note that, in the absence of selection, more than 50 per cent of the F_1 crosses gave a higher yield than the highest yielding seedling progeny of four standard varieties. The superior yielding ability of these F_1 crosses can be illustrated in another manner. The average yield of the 57 inbred lines was 58 bushels per acre; of the seedling families of the four standard varieties 75.5 bushels per acre; and of the 47 F_1 crosses 93.2 bushels per acre.

DISCUSSION

In a previous publication (Krantz, 3) it was pointed out that the employment of the method of "selection in self-fertilized lines" was particularly appropriate in a vegetatively propagated crop such as the potato. The studies presented in this paper have been concerned with the soundness of the general principle in its specific application to the improvement of the potato, and in establishing economical and effective methods for its application.

The object of selection in self-fertilized lines of potatoes is to secure fertile breeding stock that breeds true for the important economic characters, and from which abnormalities and other undesirable characters have been eliminated. The problem is essentially one of developing superior individuals for breeding purposes. The value of these individuals will not depend upon their own performance but upon their breeding behavior as ascertained by a study of their progeny and upon their ability when crossed with each other to produce individuals of economic value.

The procedure followed in producing these individuals is both analytical and synthetic. The desirable features of our commercial varieties must be separated from the undesirable; then by a building-up process individuals of the desirable types must be constructed. Inbreeding is the genetic method of analysis. It exposes characters and shows in what degree of purity these characters exist within the individual, thus enabling a selective process to separate the desirable elements into pure line groups. By crossing, these groups may then be split up and recombined to meet specific requirements. The above process is a method by which a concrete objective may be attained; at the same time it lays the foundation for a subsequent higher objective. The process of constructing breeding material and the introduction of improved combinations of characters to replace economic varieties will necessarily progress simultaneously, as the latter must be used in measuring the progress made toward the first objective. Perfection in breeding stock and in varieties may be an infinite aim. This, however, is immaterial as long as progress in the improvement of breeding stock is reflected in the production of better varieties.

SUMMARY AND CONCLUSIONS

1. The prevalence of non-fruitfulness in the potato is primarily responsible for the paucity of potato breeding work. The non-fruitfulness due to flower dropping has been eliminated by transferring the seedlings after their first year to a more favorable environment. The failure to set fruit because of pollen abortion has been overcome by inbreeding partially fertile varieties and by crossing sterile and weak pollen-producing varieties with fertile seedlings and then inbreeding the F_1 generation. Pollen sterility is eliminated from these future generations through its lethal effect on the pollen grains that carry it and through the elimination of the non-fruiting individuals of the progeny. Because the eggs are not affected, and consequently transmit the sterility to succeeding generations, the process of elimination is slower than it otherwise would be. The increase in fertility is, however, marked after the second and third inbred generations.

2. The effect of inbreeding on commercial varieties of the potato is, first to expose their heterozygous condition. After the first generation an appreciable reduction in variability is noted. In the third and fourth generations, lines begin to show sufficient uniformity that their individuality can be recognized.

3. A reduction in vigor accompanies the approach of the lines to homozygosity, as is indicated by smaller vine growth and decreased

yields. The reduction in yield for the two varieties in which lines have been inbred for four or more generations has been approximately 40 per cent below the yield of the first inbred generation. The results obtained from crosses between varieties and between inbred seedlings show that the loss in yield occasioned by inbreeding can be regained and in many cases reduced by appropriate recombinations. Two crosses between inbred lines have been carried to the F_3 generations. The difference in yield between the F_2 and the F_3 generations is approximately equal to that between the first and second inbred generations of a variety.

4. Most of the important economic characters are fairly easy to fix in the inbred lines. The process is one of discarding the poorer seedlings and lines. However, early maturity as a genetic character has been found difficult to isolate. Results from selfed and crossed progenies suggest that its expression is dependent upon dominant multiple factors. A study of the seedling progenies of standard varieties shows distinct differences between the progeny of Bliss Triumph, Irish Cobbler, and Early Ohio. The varieties studied may be ranked according to the earliness of their seedlings as follows: Bliss Triumph, Irish Cobbler, Early Ohio, Green Mountain, and Lookout Mountain. Rural New Yorker, from its behavior in crosses, appears to be genetically slightly earlier than Green Mountain.

The genetic data obtained from self-pollinating and crossing of standard varieties enable the following conclusions to be drawn: Where a wide difference in maturity exists between varieties, such as between early and late maturing ones, their seedling progenies will show the same relative difference. However, varieties of relatively the same period of maturity such as Triumph, Cobbler, and Early Ohio, may show distinct differences in their genetic constitution in regard to earliness. It would be desirable, therefore, in selecting for early maturity, to select first on the basis of individual behavior, and second on the ability to transmit this character to its seedlings. A handicap in making selections on this basis results from the high degree of sterility found in the progenies of the early varieties. A method consisting of crossing the earliest available fertile seedlings with the early varieties and selecting from later generations derived from these crosses has enabled the isolation of lines in which earliness equal to that of the progeny from the early varieties is combined with relatively high fertility. Doubtless lines homozygous for earliness can be isolated from this material.

5. A study was made to determine the importance of yield as a character to be considered when selecting inbred lines. A comparison in 1927 of the yield of 18 F_1 crosses with the yield of the parents gave a correlation coefficient of 0.556 ± 0.108. This suggests the

possibility of an important relationship. A comparison of the yield of F_1 crosses with the yield of inbred lines and seedling families of the Triumph, Cobbler, Early Ohio, and Green Mountain varieties indicates that a high yield can probably be obtained upon recombining the inbred lines even if no selection for high yield is practiced in them. The average yield of 57 inbred lines was 58 bushels per acre; of the seedling families of the four standard varieties, 75.5 bushels per acre; and of the 47 F_1 crosses made from lines picked at random, 93.2 bushels per acre. The most economical procedure appears to be to determine by actual trial the best recombinations and to select the best individuals from the highest yielding recombinations for a comparative test with the standard varieties to determine which individuals would be of value in commercial production.

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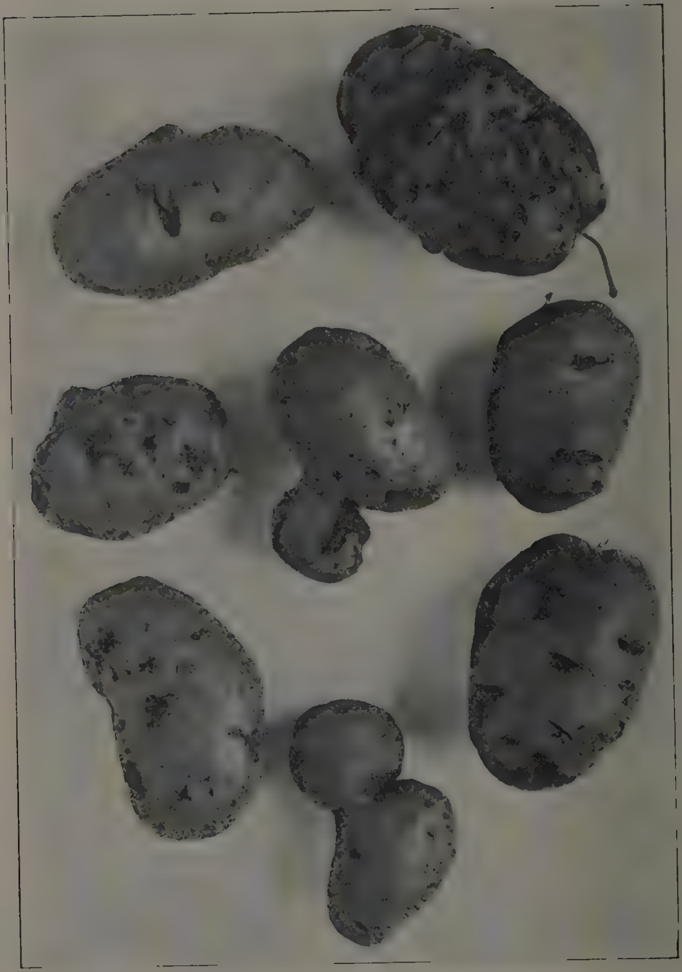

Plate 1. Tendency of Early Ohio Potatoes to Form Knobs

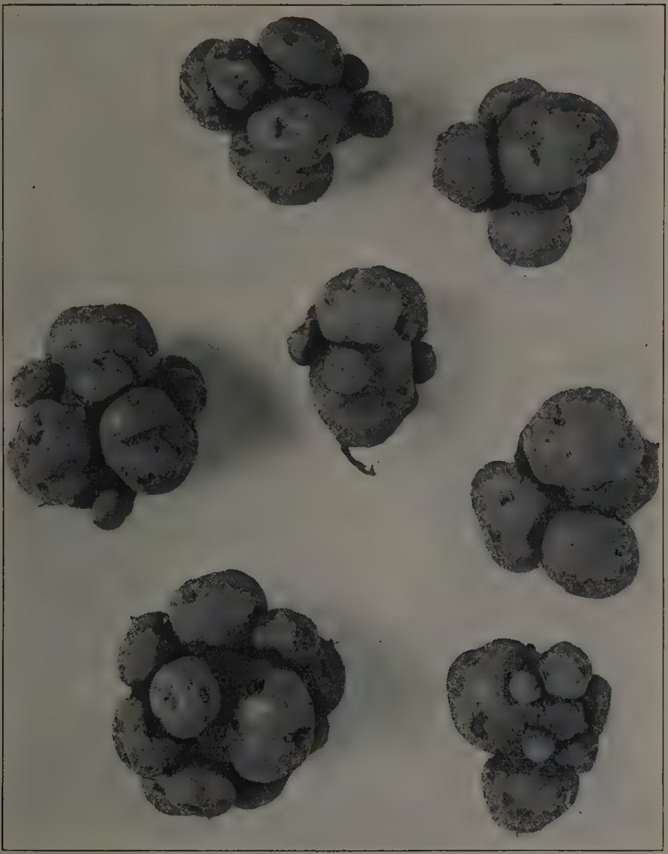

Plate 2. Early Ohio Seedling Showing Extreme Tendency Toward Development of Knobs

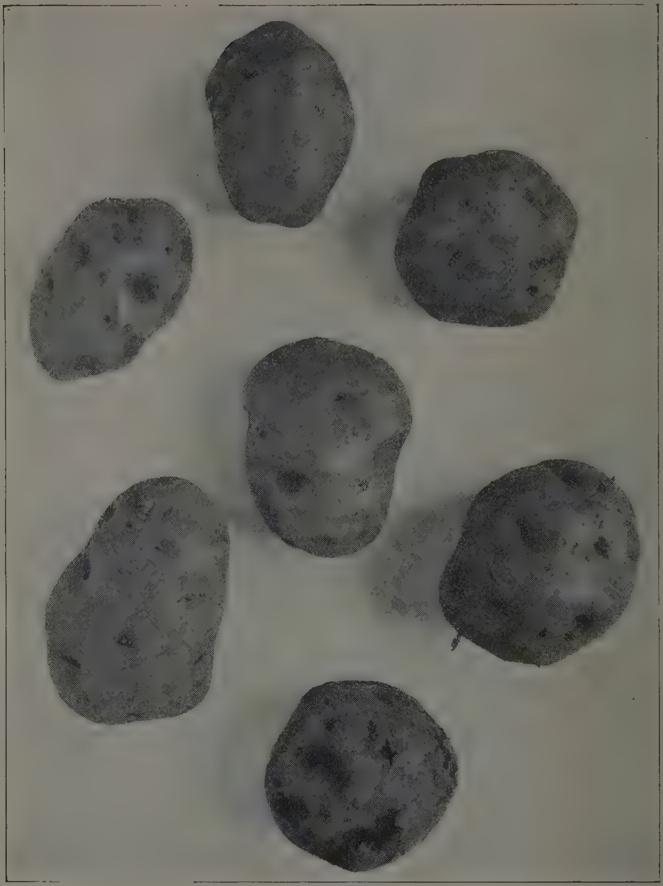

Plate 3. Early Ohio Seedling that Produces Smooth Tubers in the Same Plot

By selecting the smooth-tubered Early Ohio seedlings and again selecting the smooth-tubered seedlings in their inbred progeny, the undesirable character for second growths can be eliminated.

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Susceptibility of Wheat Varieties and Hybrids to Fusarial Head Blight in Minnesota

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SUSCEPTIBILITY OF WHEAT VARIETIES AND HYBRIDS TO FUSARIAL HEAD BLIGHT IN MINNESOTA

J. J. Christensen, E. C. Stakman, and F. R. Immer

INTRODUCTION

The only effective method of controlling wheat scab (Fusarial head blight) is to grow resistant varieties. While cultural methods will reduce losses somewhat, they can not be depended upon to control the disease adequately. With the increase in acreage of corn in the spring wheat area, Fusarial head blight is likely to become even more prevalent and destructive than it now is. The use of resistant varieties of wheat will therefore assume increasing importance. It will be necessary either to grow resistant varieties already available or to develop new ones. In either case a knowledge of the relative resistance of varieties now in existence will be very valuable. Therefore the tests described in this paper were made.

Relatively little has been done in determining varietal resistance of wheat to scab. Arthur (2), in 1891, was the first to report differences in varietal susceptibility to Fusarial head blight of wheat. Schmitz (14), Atanasoff (3), MacInnes and Fogelman (13), Hurd (11), Hayes (10), Stakman, Lambert, and Flor (17), and Wollenweber (19) have called attention to varietal differences, but none reported extensive studies. Christensen and Stakman (7), in a preliminary note, reported marked differences in susceptibility of varieties of durum and common wheats. They also found that certain strains from crosses between susceptible and resistant parents were as resistant as the resistant parent. Recently Scott (15) reported the results of tests with winter wheats that had been inoculated artificially with *Gibberella saubinetii* (Mont.) Sacc.

MATERIALS AND METHODS

During the last nine years more than 350 spring varieties, selections, and hybrids of *Triticum spp.* have been tested for relative susceptibility to scab at University Farm, St. Paul, Minnesota.[1] Most of them were tested for at least three years, some for one or two years, and a few for nine years. Fifty of the varieties were tested also at the branch experiment station at Waseca,[2] for two years. Varieties and selections grown for at least three years and a few newly developed varieties resistant to stem rust grown for one year only are included in the tabulated results (Tables I, II, III, and IV).

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[1] Most of the varieties were obtained originally from J. H. Martin, Office of Cereal Crops and Diseases, U. S. Dept. of Agr., and a few were obtained from A. C. Arny, Division of Agronomy and Plant Genetics, University Farm. The crosses, Marquis x Preston, etc., listed in Table III, were furnished by Dr. Hayes, Division of Agronomy and Plant Genetics. These were made by Dr. Hayes in 1915 with the hope of producing a variety of wheat more resistant to scab than Marquis, yet having the desirable agronomic characters of Marquis.

In 1925, the varieties listed in Table I were grown in single rows, in 1926 a second planting of the same varieties was made about two weeks later than the first, and in 1927 they were grown in uniformly replicated rows. The varieties listed in Table III were grown in duplicate plots at University Farm, three 5-foot rows of each variety in a plot. At Waseca the same varieties were grown in replicated single rod rows. At University Farm the plants were artificially inoculated. They were sprayed with a suspension of spores of *Fusarium spp.* at intervals of a day or two from the time of heading until the semi-hard-dough stage. When the weather was especially dry the plants were sprayed late at night. Most of the inoculum was obtained from material collected at different places in Minnesota, but some was obtained from other states. The pathogene was isolated from some of the collections and grown on potato dextrose agar or on a mixture of autoclaved wheat and oats. Some inoculum was obtained by making washings of diseased spikelets of wheat gathered the previous season. No attempt was made to use only one species or strain of the scab-producing organisms, because it was hoped to determine the reaction of the varieties to as many as possible. The plants at Waseca were not inoculated artificially.

Counts to determine the percentage of affected heads were made shortly before the wheat ripened. The percentage was usually based on counts of 200 heads (Table III), but in some cases (Tables I and II) it was based on a smaller number, particularly when the varieties were severely affected. The percentage of infected seed was determined by examination of scabby heads in the laboratory.

RESULTS

All of the 350 varieties and selections of *Triticum vulgare, T. durum, T. compactum, T. dicoccum, T. turgidum, T. spelta,* and *T. polonicum* became infected to a greater or less degree. None were immune. At least some varieties within all these group species were susceptible. The percentage of infected heads in the different varieties ranged from a bare trace to 100.

It is evident from Tables I, II, and III that the common wheats as a class are more resistant than the durums, altho some of the common wheats are very susceptible. In 1927 the percentage of blighted heads in common wheats ranged from 1 to 78 and in 1928 from 6 to 93. The following were among the most susceptible: Chul, Bunyips, Emerald, Federation, Gypsum, and Propo. Marquis, the most popular variety in the hard red spring wheat region, and Marquillo, a promising rust-resistant variety, were susceptible. The following were very resistant: Converse, Glyndon Fife, Haynes Bluestem, Huston, Jumbuck, Lodoga, Norka, Rysting, Wellman, and White Fife.

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[2] The writers are indebted to R. E. Hodgson, Superintendent of the Southeast Experiment Station, for growing these varieties at Waseca.

The average percentage of infected heads of Glyndon Fife during seven seasons (Table II) was 4.0 in contrast with 26.7 of Kitchener and 22.1 of Marquis. Kota was intermediate, the infection being 17.4 per cent for the same period (see Fig. 1).

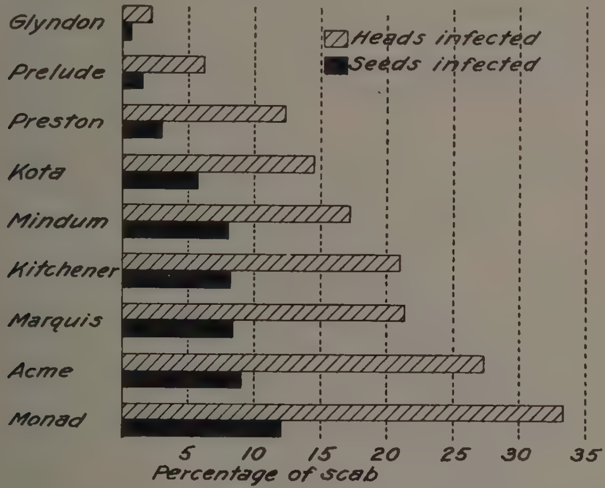

Fig. 1. Average Percentages of Fusarial Head and Seed Blight on Nine Varieties of Wheat Artificially Inoculated at University Farm 1921-23 and 1925-27 Inclusive

The durum wheats as a class were decidedly more susceptible than the common wheats. In 1927 the percentage of infection on different varieties of durum ranged from 1 to 100, altho most of the more than 200 varieties tested from 1925 to 1928 were susceptible. Some of the most susceptible were Adjini, Negro, Potia Nadiad, and Souri. The following were resistant: Batum, Medeah, and C. I. 3198. Mindum, Minn. 470, appears to be the most resistant of the durum varieties commonly grown in Minnesota and the Dakotas. The average percentage of infected heads in this variety for seven years was 25.0 as compared with 40.1 for Monad and 36.3 for Acme (See Table II).

There were differences also in the susceptibility of strains within a variety. For example, four selections of Kubanka, C. I. 1440, differed considerably in this respect. The average for infected seed of one selection of this variety for 1926 and 1927 was 7.7 per cent, while that of another selection was 28.7 per cent for the same two-year period (Table I).

An attempt was made to determine the behavior of crosses between susceptible and resistant parents. In Table III is summarized the behavior of 38 hybrids. These crosses were tested at Waseca from 1923 to 1925 inclusive, and at University Farm from 1923 to 1927 inclusive. In 1924 no notes were taken at either place because little scab developed, and there was a severe epidemic of head blight caused by other factors than scab. Some hybrids were resistant at both Waseca and University Farm, others were susceptible at both places, while still others were susceptible at one place but resistant at the other. Most of the crosses were intermediate in their reaction to scab, altho some of the lines obtained from Marquis x Preston crosses and some from Marquis x Haynes Bluestem crosses were as resistant as the resistant parent. The Preston parent used in the Preston x Marquis crosses was not Preston, Minn. 924, but a selection from it. Its reaction to scab, according to a preliminary test, was apparently identical with that of Preston, Minn. 924. These hybrids were purified strains; the original crosses were made by Dr. H. K. Hayes in 1915.

Eight rust-resistant varieties of wheat, developed from crosses between Kota and Marquis, were tested in 1928. All were very susceptible to Fusarial head blight. The percentage of infection ranged from 44.5 to 88.5, while in Marquis it was 28.3 and in Kota 34.0.

The writers observed no gross morphological characters within any class of wheat that could be correlated with resistance or susceptibility. Schmitz (14) concluded that awnless varieties of common wheats were more susceptible than awned varieties and that pubescent varieties were the most susceptible of all. The writers found no apparent correlation between reaction to head blight and pubescence and the presence or absence of awns. Nearly all the durums tested were awned, and, as previously stated, they were very susceptible as a class. Selections within a variety that do not differ greatly in morphological characters often react differently toward scab, thus supporting the observation that there is no obvious correlation between reaction to scab and morphological characters. Furthermore, some of the susceptible lines from Marquis x Haynes Bluestem crosses resembled the susceptible parent in morphology, while others resembled the resistant parent. This was true also of selections from the Marquis x Preston cross.

It is evident from Tables I, II, and III that there are marked differences in the degree of infection in the same varieties when grown the same year at Waseca and University Farm and also when grown at the same place in different years. Statistical studies were made to determine the degree of correlation between the percentages of infection of the same varieties grown at different places in the same year and in the same place in different years. All calculations were carried to four decimal places, and the number was then reduced to that suggested by Kelley (12). Results are given in Table IV. All the correlation coefficients given in the text are based on calculations in which the percentage of scab infections was carried to tenths of a per cent. The reaction of the varieties presented in Tables I, II, and III are given to only the nearest whole number.

The average percentages of infected seeds for the varieties tested at Waseca in 1923 and 1925 were 1.2 and 1.1 respectively. The correlation between the infections for these two years was + .65 ± .06 (Table IV). The average percentage of seed infection for the same varieties and strains at University Farm was 0.4 and 4.9 respectively. In this case the correlation coefficient was + .35 ± .09. Apparently the conditions for infection were more nearly the same for the two years at Waseca than at University Farm. It is of considerable interest that a correlation coefficient of + .65 ± .06 was obtained, when the mean percentages of infected seeds were only 1.2 and 1.1 for the two years correlated. Apparently reaction to scab at Waseca was strongly inherited under the conditions of the experiment. The lower correlation at University Farm may be partly explained by the low percentage of infection in 1923—so low that it was difficult to determine statistically whether the varieties grown were really resistant or had merely escaped infection. A higher correlation was obtained between percentages of seed infection of the same strains at Waseca and University Farm in 1925 than in 1923, as shown by the correlation coefficients of + .59 ± .04 and + .42 ± .08 respectively.

At University Farm in 1925 and 1926 the average percentages of infected heads were 29.6 and 8.2 respectively, while the average percentages of infected seeds were 7.4 and 3.1 for the same varieties. The correlation coefficient for seed infection was + .22 ± .10 and for head infection + .15 ± .10. Neither can be considered statistically significant. The same strains and varieties were grown in two series in 1925, one series being planted two weeks later than the other. The average percentage of infected heads for the first series was 29.6 and for the second 5.1. The correlation for percentage of heads infected in the two plantings was + .19 ± .10. The average percentages of infected seeds in the same varieties were 7.2 and 2.2 respectively, and a correlation coefficient of + .38 ± .09 was obtained for the two plantings. Apparently time of planting has a very marked effect on the reaction of varieties to scab infection. From 1925 to 1927, inclusive, a much larger number of varieties were tested at University Farm. The average percentage of heads infected for 71 varieties of vulgare wheats was 10.1 in 1926 and 15.7 in 1927; for the durum wheats it was 12.7 per cent and 52.4 per cent respectively, for the same two years. The average percentage of infected seeds for the same vulgare varieties was 4.4 in 1926 and 8.3 in 1927; for the durum varieties, 6.7 in 1926, and 30.3 in 1927. Correlation coefficients of + .02 ± .08, + .06 ± .05, + .06 ± .05, and + .05 ± .05 (Table IV) were obtained for both head and seed infection when the reactions of these strains of wheat to scab in 1926 and 1927 were correlated. It is evident that there was no significant correlation between the percentages of infection in 1926 and 1927, when the percentage of either infected heads or infected seeds was considered.

An attempt was made to determine whether there was a correlation between the severity of head blight and the percentage of seeds infected. The results are summarized in Tables V, VI, and VII. The correlation between two series, A and B, of 116 varieties of durum planted at the same time was essentially the same whether the percentages of infected heads or of seeds were used in calculating the correlation coefficient. They were respectively + .66 ± .04 and + .62 ± .04. There was a correlation of +.91 ± .02 between the average percentage of heads infected and the average percentage of seeds infected in 41 varieties grown at Waseca in 1926 and 1927. In a similar study of the 41 strains grown for three years and for 71 vulgare and 154 durum varieties grown for two years at University Farm, correlation coefficients of + .87 ± .03, + .92 ± .01, and + .86 ± .01 were obtained. Further, there was a correlation of + .87 ± .01 between the average percentage of heads infected and of seeds infected in the 116 varieties of durum wheat grown in two systematically distributed plots at University Farm in 1927. Blakeman's test was applied to each of these correlations, and regression was found to be essentially linear.

One of the primary purposes of this study was to determine the extent of inheritance of reaction of wheat varieties to scab infection. In the studies reported here no significant difference could be demonstrated between correlation coefficients obtained from heads infected and seeds infected in the same varieties and lines grown from year to year or in different series grown in the same year. The correlation coefficient of + .65 ± .06, obtained from the percentage of seeds infected in the same 41 strains grown in 1923 and 1925 at Waseca, and of + .35 ± .09 obtained when the same varieties were grown at University Farm in those years, indicates that in these cases the factors for inheritance apparently played a far more important part in determining reaction at Waseca than at University Farm.

No significant correlation coefficients were found between reactions of either vulgare or durum varieties grown at University Farm in

1925 and 1926 or in 1926 and 1927. Apparently conditions for infection of these varieties in 1925 and 1926 or in 1926 and 1927 were quite different.

From the correlation of + .87 ± 0.2 between the average percentages of head infection and seed infection in 116 durum wheat varieties grown in two plots the same year, the percentage of seeds infected in a given variety can be predicted with considerable accuracy if the percentage of infected heads is known. (In this case the percentage of seeds infected ranged from 3 to 87.) For practical purposes, in view of the much greater ease with which notes may be taken on heads infected, and the fact that all correlation coefficients determined between percentages of heads and seeds blighted were at least + .86, it seems fair to conclude that data on head infection in Minnesota may replace notes on seed infection.

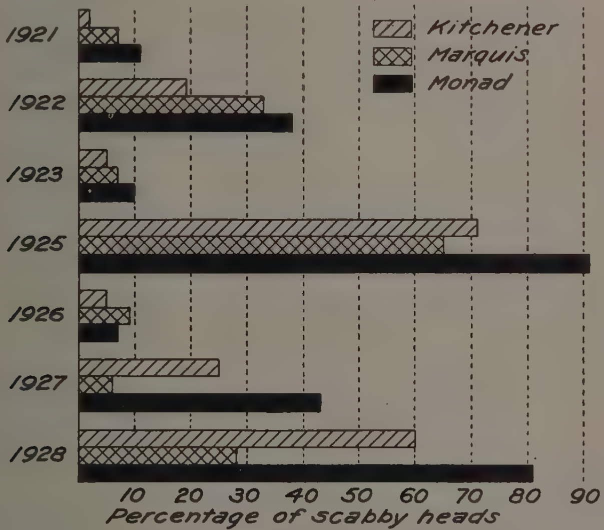

Fig. 2. Fluctuation in the Development of Fusarial Head Blight on Three Varieties of Wheat Artificially Inoculated at University Farm 1921-23 and 1925-28 Inclusive

The degree of scab infection in the same varieties may vary greatly from season to season (see Fig. 2). In 1926, at University Farm, the percentages of infected heads were 3.3 for the durum variety Sineuska, C. I. 4010; and 1.0 for Kubanka 8, C. I. 4063; but in 1927 they were 100 and 57.8 respectively. On the other hand, Reward, John Brown, and Marquillo were much more severely infected in 1926 than in 1927 (Table I). Preston was resistant four years out of seven and Monad fairly susceptible five years out of seven at University Farm (Table II). It is evident from the low and statistically nonsignificant correlation coefficients obtained in these studies that several variables strongly influence the percentage of infection. It seems probable that these variables may be meteorological conditions and the prevalence of different species or physiologic forms of the pathogenes.

Head blight of wheat may be caused by several species of *Fusarium*. Atanasoff (4) lists 7 species that may cause head blight and several others that may cause root rot, and points out that the different ones may have different geographic distribution. For example, *Gibberella saubinetii* (Mont.) Sacc. commonly causes scab in the United States, Bulgaria, and Southern Russia; *F. avenaceum* (Fr.) Sacc. commonly causes scab in Northern Russia. Atanasoff concluded that approximately 50 per cent of the head blight in Holland was caused by *F. culmorum* (W. G. Sm.) Sacc., altho he found *G. saubinetii* also on about 40 per cent of the infected heads. Both species were common in Germany, where *Calonectria graminicola* (Berk. & Brm.) Wr. is said to cause a considerable amount of Fusarial head blight of wheat. Dickson, Johann, and Wineland (8) concluded that 94 to 98 per cent of the head blight of wheat in the central and eastern states of the United States was caused by *G. saubinetii*. Preliminary studies by Tu (18) indicate that this is not always true for Minnesota. In 1926 he repeatedly isolated several pathogenic species of *Fusarium* from scabby wheat. It seems clear, therefore, that several species of *Fusarium* may cause head blight of wheat. Furthermore, as shown by Tu (18), there are striking differences in the temperature requirements of some of these species. Obviously, then, considerable variation in the degree of infection of varieties in different seasons and different localities may be expected.

Not only do different species of *Fusarium* cause head blight and seed blight, but there is evidence of physiologic specialization within some of these species. Greaney and Bailey (9) found at least four different cultural forms of *G. saubinetii*. Two of these were virulent pathogenes; the others were much less virulent. Tu (18) was able to distinguish three physiologic forms of *F. culmorum* by their cultural characters and parasitic effect on heads of wheat and barley. It seems likely that there are many physiologic forms of several of the species of *Fusarium* which cause head blight and seed blight. This fact would partially explain the variability in the apparent resistance of varieties at different times and in different places.

Not only are there physiologic forms of some of the wheat scab pathogenes, but it is likely that new ones are being produced. Physiologic forms of some fungi have been shown to mutate frequently. For example, mutation occurs very commonly in the smut fungi, particularly *Ustilago zeae* (Beck.) Ung. (16) and some of the Fungi Imperfecti such as *Helminthosporium sativum* P., K. and B. (6). Brown

(5) has shown that mutation is fairly common in certain species of *Fusarium.* Recently Tu (18) observed mutation in *F. culmorum,* a virulent pathogene on wheat and barley in Minnesota. It seems likely, then, that the virulence of physiologic forms of various species of *Fusarium* may be changing considerably as a result of mutation.

Meteorological conditions also constitute an important variable that probably accounts for some differences in behavior of varieties with respect to scab. For example, Marquis wheat becomes heavily infected with scab in many years in southern Minnesota. At St. Paul, however, one may spray this variety repeatedly with a suspension of conidia of various scab organisms and yet in certain years little infection results. In the northwestern section of the state there seldom is more than a bare trace of Fusarial head blight. This may be due partly to the fact that relatively little corn is grown in that region. On the other hand, precipitation and temperature are quite different in northwestern and in southern Minnesota. The effect of meteorological conditions on the development of scab is shown further by experiments made for four years at University Farm. The same varieties of wheat were grown on uniform land but were sown at different dates (Table VIII). In 1923, for example, the average percentage of head infection for 52 varieties sown on April 27 was 4.9 and for the same varieties sown a week later it was 3.1, and there was almost no scab when these varieties were sown two weeks later. In 1925 and 1926 there was the same general ratio between the percentages of infected heads in the plots sown at different dates, altho the percentages of infection were higher than in 1923. In 1927, however, conditions were reversed. There were 5.7 per cent of blighted heads in Marquis and 43 per cent in Monad sown on April 29. But in Marquis and Monad sown on May 6 infection was 100 per cent. When sown one week later, May 13, the two varieties were still severely infected, the percentages being 86.7 and 96.5 respectively. In 1925, on the other hand, only 1.5 and 0.5 per cent of the heads were infected in Marquis and Monad sown on May 6. The same general relationship held for percentages of infected seed.

Rainfall appears to be one of the most important meteorological factors influencing the degree of infection. This is borne out by numerous field observations made by the writers and other investgators. Atanasoff (4), Scott (15), and others have concluded that an abundance of moisture is conducive to Fusarial head and seed blight. It has been supposed that rainfall is most effective in promoting infection when it falls at flowering time or shortly thereafter. According to Dickson, Johann, and Wineland (8), initial infection occurs principally through the anthers of the stamens. Adams (1) found the first evidence of infection in the developing embryo. Atanasoff (4) maintains that infection may take place as readily soon after the disappearance of the anthers as earlier. In his experiments, infection resulted from artificial inoculations made at any time from flowering until the medium-dough stage, altho he concluded that the host was most susceptible at flowering time and shortly thereafter. He is of the opinion that infection does not necessarily take place through anthers but may take place at any point on the spikelets where suitable contact can be made between the pathogene and the host. It seems likely, therefore, that abundant rainfall from blossoming time until the dough stage would be conducive to the development of scab.

Weather conditions also influence the progress of the disease after the infection has taken place. The pathogene usually spreads rapidly when a few hot rainy days follow the flowering period of wheat, and symptoms of the disease appear within a few days. If conditions remain favorable for the development of the pathogene, it may extend 5 or 10 cm. and sometimes farther down the stem of the infected plant. Consequently the heads often ripen prematurely. Even under favorable conditions, the rate of spread of the pathogene and the symptoms differ in different varieties. The discoloration of the peduncle may be gray in some varieties, brownish in others, and creosote-like in still others. Fairly high humidity is essential for the production of conidia on infected plant parts. Severe infection, however, may occur without any conspicuous signs of sporulation. Sporulation usually is not abundant on infected varieties at University Farm.

There is always a possibility that varieties may escape infection. This undoubtedly is true of some of the varieties grown in 1925, 1926, and 1927. In 1927, for example, most of the early maturing varieties were relatively free from infection, altho they had been heavily infected the previous season. This was true particularly of Reward, Red Sask., and Quality (Table I). Arthur (2) found that head blight was more severe on late-maturing than on early-maturing varieties, and that delayed maturity of early varieties resulted in heavy infection. This may be true for certain varieties and certain regions, but it is not universally true. The durum wheats as a class mature later than the common wheats and are more susceptible to scab, but resistance within the durum class is not correlated with the time of heading or with the date of maturity. The same is true of the common wheats.

SUMMARY

1. During the last nine years more than 350 spring varieties, selections, and hybrids of *Triticum spp.* have been tested for relative susceptibility to Fusarial head and seed blight at University Farm, St. Paul, Minnesota. Fifty of these varieties were tested at Waseca, Minnesota, also.

2. All of the 350 varieties, selections, and hybrids became infected to a greater or less degree..

3. The common wheats were more resistant than the durums, altho some were very susceptible. There was considerable variation in resistance to scab in the durums also.

4. A study was made of the behavior of crosses between susceptible and resistant parents at University Farm, St. Paul, and at Waseca, Minnesota. Most of the hybrids from Marquis x Preston and from Marquis x Haynes Bluestem were intermediate in their reaction to scab. Some of the lines were as resistant as the resistant parent. All the Kota x Marquis crosses studied were susceptible.

5. No apparent gross morphological characters within any class of wheat appeared to be highly correlated with resistance or susceptibility.

6. No statistically significant differences could be demonstrated between correlation coefficients obtained from heads infected and seeds blighted in the same varieties and lines grown in different years, or in two different series in the same year. The correlations between the percentages of heads blighted or seeds blighted in the same varieties ranged from + .86 ± .01 to + .92 ± .01. Therefore it seems fair to conclude that, for practical purposes, data on head infection may be used to replace notes on seed infection in Minnesota.

7. It was evident from the very low and statistically nonsignificant correlation coefficients obtained between the percentages of infection in varieties grown in the same year but sown at different times, or grown at the same place in different years, or at different places in the same year, that a number of variables strongly influenced the percentages of infection. These variables were probably differences in meteorological conditions and in the prevalence of different species and physiologic forms of the pathogenes.

8. Considerable caution is necessary in drawing conclusions from the results of varietal tests unless they are conducted for several years under carefully replicated and controlled conditions.

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TABLE I

PERCENTAGE OF FUSARIAL HEAD AND SEED BLIGHT ON WHEAT VARIETIES INOCULATED ARTIFICIALLY IN THE FIELD AT UNIVERSITY FARM, ST. PAUL, MINNESOTA, 1925-27 INCLUSIVE

Species and varieties	C. I. No.	Degree of infection, 1925	Percentage of heads infected*			Percentage of seeds infected		
			1926	1927	Av.	1926	1927	Av.
Triticum vulgare								
Baart	1697	T†	5	19	12.0	1	9	5.0
Bobs	4991	M	20	14	17.0	7	4	5.5
Bunyip	5125	H	27	39	29.5	11	16	18.5
Canadian Red	6282	..	24	39	31.5	13	16	14.5
Ceres	6900	..	20	17	18.5	9	5	7.0
Champlain	4782	M	3	23	13.0	2	8	5.0
Chul	2227	H	57	..	....	33	..	....
Colorado No. 50	4959	..	12	14	13.0	8	6	7.0
Converse	4141	M	1	2	1.5	T	T	T
Defiance	6477	M	1	18	9.5	1	13	7.0
Dicklow	3663	M	9	28	18.5	3	22	12.5
Early Defiance	6480	M	15	5	10.0	5	1	3.0
Early Red Fife	4932	H	5	11	8.0	2	6	4.0
Emerald	4397	T	4	55	29.5	1	24	12.5
Erivan	2397	..	11	3	7.0	2	1	1.5
Federation	4734	H	6	78	42.0	2	56	29.0
Foisy	5242	M	0	15	7.5	0	7	3.5
Galgalos	2398	..	4	32	18.0	2	17	9.5
Ghirka	1517	T	18	5	11.5	9	2	5.5
Glyndon	2870	L	0	5	2.5	0	1	0.5
Gypsum	4762	M	23	57	40.0	14	37	25.5
Hard Federation	4980	M	14	21	17.5	8	11	9.5
Haynes Bluestem	2874	T	0	2	1.0	0	2	1.0
Humpback	3690	M	0	31	15.5	0	19	9.5
Huron	3315	..	2	3	2.5	T	1.0	0.5
Huston	5208	T	6	1	3.5	3	1.0	2.0
Indian	4489	H	1	21	11.0	1	10.0	5.5
Java	4966	..	13	3	8.0	5	2.0	3.5
John Brown	2397	..	33	1	17.0	14	1.0	7.5
Jumbuck	4608	T—	1	1	1.0	1	1.0	1.0
Kitchener	4800	H	5	25	15.0	2	10.4	6.0
Kota	5878	T	6	4	5.0	2	2.0	2.0
Ladoga	4795	..	1	2	1.5	T	1.0	0.5
Laramie	6235	..	1	5	3.0	T	4.0	2.0
Lynn	6346	M	13	16	14.5	7	8.0	7.5
Marquis	3641	H	9	6	7.5	4	3.0	3.5
Marquis x Kanred, Minn. 2219	....	..	2	15	8.5	T	6.0	3.0
Marquis x Kanred, Minn. 2223	....	..	8	14	11.0	2	8.0	5.0
Marquis x Kanred, Minn. 2121	....	..	16	21	18.5	4	5.0	4.5
Marquis x Kanred, Minn. 2220	....	..	8	17	12.5	2	10.0	6.0
Marquis x Kota 1656	....	..	19	11	15.0	8	6.0	7.0
Marquillo, Minn. 2202	....	M	42	14	28.0	10	2.0	6.0
Mexican Bluestem	6004	H	4	46	25.0	2	16.0	9.0
New Zealand	6011	L	1	28	14.5	1	23.0	12.0
Norka	4377	M	2	1	1.5	T	T	T
Pacific Bluestem	4067	..	5	8	6.5	1	3.0	2.0
Palisade	4798	L	1	15	8.0	T	5.0	2.5

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* The percentages in the table for 1926 and 1927 were reduced to the nearest whole number. The correlation studies in the text are based on calculations in which the percentages were carried out to the nearest tenth.

† T = Trace, L = Light, M = Moderate, H = Heavy.

TABLE I—*Continued*

PERCENTAGE OF FUSARIAL HEAD AND SEED BLIGHT ON WHEAT VARIETIES INOCULATED ARTIFICIALLY IN THE FIELD AT UNIVERSITY FARM, ST. PAUL, MINNESOTA, 1925-27 INCLUSIVE

Species and varieties	C. I. No.	Degree of infection, 1925	Percentage of heads infected*			Percentage of seeds infected		
			1926	1927	Av.	1926	1927	Av.
Parkers Marquis Minn. 2222	....	..	17	6	11.5	1	4.0	2.5
Pioneer	4324	T—	6	2	4.0	2	2	2.0
Power	3697	L	1	5	3.0	1	3	2.0
Prelude	4323	..	7	8	7.5	3	3	3.0
Preston	3328	T	4	8	6.0	1	4	2.5
Progress, Minn. 2225	....	..	11	4	7.5	3	1	2.0
Propo	1970	T	1	68	34.5	1	37	18.0
Quality	6157	M	20	6	13.0	3	3	3.0
Red Bobs	6255	H	36	17	26.5	23	9	16.0
Red Fife	3329	H	4	7	5.5	1	2	1.5
Red Sask., Minn. 2193	....	..	23	4	13.5	7	2	4.5
Reseca	6390	M	0	9	4.5	0	5	2.5
Reward, Minn. 2204	....	..	34	0	17.0	10	0	5.0
Rink	5868	H	0	17	8.5	0	13	6.5
Ruby	6047	..	14	2	8.0	6	1	3.5
Rysting	3022	L	1	3	2.0	T	1	0.5
Sonora	3036	M	5	31	18.0	4	20	12.0
Stanley	4796	M	10	4	7.0	3	1	2.0
Surprise	2986	M	13	8	10.5	6	6	6.0
Touse	6047	H	1	26	13.5	1	17	9.0
Webster	3780	..	23	58	40.5	9	26	17.5
Wellman	4144	M	0	3	1.5	0	1	0.5
White Federation	4981	M	35	4	19.5	19	2	10.5
White Fife	4412	L	0	5	2.5	0	3	1.5
Triticum durum								
Abl-el-Kodar	2075	M	2	65	33.5	1	41	24.0
Acme	5284	..	6	35	20.5	5	20	12.5
Adkini	1594	..	10	55	32.5	6	28	17.0
Adjini	4594	H	15	93	54.0	12	47	29.5
Agini	3844	H	14	71	42.5	9	36	22.5
Akrona	6881	M	7	35	21.0	2	24	13.0
Albacete	2091	..	2	28	15.0	1	11	6.0
Allemond	4595	T—	13	67	40.0	11	43	27.0
Anchuelo	3280	H	3	32	17.5	3	28	15.5
Arnautka	1493	M	7	16	11.5	3	11	7.0
Arnautka	1431	M	4	23	13.5	3	11	7.0
Arnautka	1537	H	25	71	48.0	14	36	25.0
Arnautka	1494	..	1	19	10.0	1	10	5.5
Azizi	4593	H	5	24	14.5	2	16	9.0
Bansi	4560	M	12	78	45.0	8	40	24.0
Batum	3096	T—	1	16	8.5	0	2	1.0
Berbern	4596	M	9	77	43.0	6	30	18.0
Beliouni	3848	M	17	66	41.5	10	34	22.0
Beliouni	3852	M	9	85	46.5	7	74	40.5
Beliouni	3842	M	0	76	38.0	0	60	30.0
Beloturka	1520	M	8	60	34.0	3	29	16.0
Bengal	5060	..	25	53	39.0	9	19	14.0
Biskra	4582	M	11	36	23.5	8	27	17.5
Black Don	1446	M	22	65	43.5	T	16	8.0
Blanca	2192	T—	16	91	53.5	5	71	38.0
Blue Beard	6128	M	0	93	46.5	0	80	40.0
Buford	5295	M	0	27	13.5	0	11	5.5
Cowra No. 16	4738	H	4	78	41.0	3	68	35.5
D-46	....	M	35	51	43.0	17	25	21.0
Deves	5476	H	17	49	33.0	6	28	17.0
Durum No. 7	3323	..	20	66	43.0	8	23	15.5

TABLE I—*Continued*

PERCENTAGE OF FUSARIAL HEAD AND SEED BLIGHT ON WHEAT VARIETIES INOCULATED ARTIFICIALLY IN THE FIELD AT UNIVERSITY FARM, ST. PAUL, MINNESOTA, 1925-27 INCLUSIVE

Species and varieties	C. I. No.	Degree of infection, 1925	Percentage of heads infected*			Percentage of seeds infected		
			1926	1927	Av.	1926	1927	Av.
Durum No. 4	3321	M	12	81	46.5	10	56	33.0
Gharnovka	1447	M	38	87	62.5	21	43	31.5
Golden Ball	5059	..	0	89	44.5	0	57	28.5
Iumillo	1736	M	4	45	24.5	2	17	9.5
Kahla	2088	M	5	24	14.5	2	13	7.5
Kahla	5529	..	2	35	18.5	1	11	6.0
Kubanka	1440	M	1	52	26.5	1	26	13.5
Kubanka	1440-74	M	2	65	33.5	T	57	28.5
Kubanka	1440-94	..	4	61	32.5	3	36	19.5
Kubanka	1440-99	M	20	70	45.0	9	54	31.5
Kubanka	1440-117	..	2	39	20.5	T	15	7.5
Kubanka	1516	H	19	37	23.0	11	26	18.5
Kubanka	1581	M	10	67	38.5	7	28	17.5
Kubanka	3715	M	4	88	46.0	1	68	34.5
Kubanka No. 8	4063	M	1	58	29.5	1	23	12.0
Lenah Khetifa	4585	..	4	22	13.0	2	9	5.5
Mahmoudi	4591	H	5	57	31.0	3	35	19.0
Mahmoudi Ag. 3 ..	4592	H	13	92	52.5	7	61	34.0
Mekki	4590	M	18	68	43.0	11	32	21.5
Marouani	1593	M	4	63	33.5	3	24	13.5
Marouani	2235	M	14	26	20.0	6	11	8.5
Marouani	5473	M	12	52	32.0	5	20	12.5
Medeah	4185	T—	6	50	28.0	2	39	20.5
Medeah	4581	M	8	7	7.5	6	3	4.5
Mindum	5296	M	5	16	10.5	2	6	4.0
Monad	3320	..	3	43	23.0	2	32	17.0
Mohamed ben Bachir	2087	M	3	80	41.5	2	66	34.0
Namira	4583	M	20	16	18.0	5	7	6.0
Negro	2090	M	22	97	59.5	13	37	25.0
Nodak	6519	..	2	40	21.0	2	16	9.0
Peliss	1584	..	12	60	36.0	4	39	21.5
Pererodka	1515	M	11	80	45.5	8	43	25.5
Potia Nadiad	4691	..	20	100	60.0	20	50	35.0
Richi	2089	M	2	87	44.5	1	68	34.5
Saragolla	2228	H	13	50	31.5	10	29	19.5
Sbei	4586	M	5	20	12.5	4	7	5.5
Sineuska	4010	H	3	100	51.5	1	89	45.0
Souri	4597	M	50	87	68.5	36	50	43.0
Taganrock	4589	T	0	35	17.5	0	23	11.5
Taganrock	3979	M	5	95	50.0	4	49	26.5
Teiskais	3266	M	9	85	47.0	2	67	34.5
Theuniseen	4184	..	3	32	17.0	1	12	6.5
White Spring	3099	M	11	82	46.5	4	41	22.5
Yellow Gharnovka	1444	M	27	46	36.5	20	26	23.0
Yellow Gharnovka	2096	M	4	55	29.5	2	27	14.5
Velvet Don	2122	M	20	68	44.0	7	41	24.0
Unnamed varieties								
	2691	M	10	15	12.5	6	7	6.5
	3069	M	31	31	31.0	7	12	9.5
	3137	M	0	78	38.5	0	65	32.5
	3138	T	0	86	43.0	0	50	25.0
	3139	H	9	74	41.5	3	32	17.5
	3141	M	0	94	46.5	0	66	33.0
	3143	M	0	38	19.0	0	14	7.0
	3144	T	14	38	26.0	9	6	7.5
	3146	M	21	93	57.0	13	52	32.5
	3147	T	6	73	39.5	5	66	35.5
	3148	T	10	27	18.5	7	13	10.0

TABLE I—*Continued*

PERCENTAGE OF FUSARIAL HEAD AND SEED BLIGHT ON WHEAT VARIETIES INOCULATED ARTIFICIALLY IN THE FIELD AT UNIVERSITY FARM, ST. PAUL, MINNESOTA, 1925-27 INCLUSIVE

Species and varieties	C. I. No.	Degree of infection, 1925	Percentage of heads infected*			Percentage of seeds infected		
			1926	1927	Av.	1926	1927	Av.
Unnamed varieties	3156	M	14	71	42.5	7	52	29.5
	3161	H	4	42	22.0	3	29	16.0
	3162	M	47	19	33.0	16	9	12.5
	3163	H	12	49	30.5	3	22	12.5
	3166	T	35	21	28.0	8	6	7.0
	3169	M	4	77	40.5	4	27	15.5
	3170	..	21	27	24.0	14	14	14.0
	3172	T	0	19	9.5	0	10	5.0
	3173	M	9	44	26.5	3	19	11.0
	3175	H	5	77	41.0	3	45	24.0
	3176	H	2	90	46.0	1	51	26.0
	3177	M	25	19	22.0	12	9	10.5
	3179	T+	3	23	13.0	0	11	5.5
	3181	H	1	44	22.5	T	16	8.0
	3184	M	4	72	38.0	1	59	30.0
	3187	M	46	22	34.0	25	7	16.0
	3190	H	0	34	17.0	0	14	7.0
	3191	M	42	50	46.0	22	17	19.5
	3192	M	5	12	8.5	5	3	4.0
	3193	M	3	1	2.0	1	T	0.5
	3195	M	4	16	10.0	1	5	3.0
	3196	M	4	27	15.5	1	14	7.5
	3197	M	0	17	8.5	0	9	4.5
	3198	M	4	3	3.5	2	1	1.5
	3199	H	2	15	8.5	T	7	3.5
	3200	H	0	18	9.0	0	10	5.0
	3207	M	1	54	27.5	T	34	17.0
	3224	H	2	10	6.0	2	6	4.0
	3226	M	22	7	14.5	8	2	5.0
	3230	H	3	28	15.5	1	10	5.5
	3231	H	6	37	21.5	4	23	13.5
	3233	H	6	50	28.0	2	32	17.0
	3234	M	1	52	26.5	T	49	24.5
	3235	M	2	26	14.0	T	20	10.0
	3236	H	0	53	26.5	0	31	15.5
	3237	H	4	90	47.0	3	47	25.0
	3238	H	20	23	21.5	6	7	6.5
	3241	H	5	68	36.5	2	32	17.0
	3242	M	14	16	15.0	1	8	4.5
	3243	M	38	75	56.5	24	58	41.0
	3244	M	18	63	40.5	6	33	19.5
	3265	M	28	46	37.0	10	28	19.0
	4074	..	11	93	52.0	11	68	39.5
	4076	M	18	70	44.0	13	44	28.5
	4526	..	28	12	20.0	16	7	11.5
	4544	M	0	81	40.5	0	49	24.5
	4917	M	27	60	43.5	12	34	23.0
	4918	..	16	26	21.0	8	8	8.0
	4919	M	29	95	62.0	26	42	34.0
	4925	M	30	48	39.0	20	32	26.0
	5094	M	3	13	8.0	2	5	3.5
	5111	..	61	32	46.5	30	8	19.0
	5112	M	0	96	48.0	0	64	32.0
	5477	M	0	76	38.0	0	61	30.5
	6130	M	11	23	17.0	6	12	9.0
Triticum dicoccum								
Vernal	1524	..	0	31	15.5	0	9	4.5
Triticum polonicum								
White Polish	3007	T	0	93	46.5	0	63	31.5

TABLE II

Percentages of Fusarial Head Blight on Nine Varieties of Wheat Artificially Inoculated in the Field at University Farm, St. Paul, Minnesota, 1921-23 Inclusive, and 1925-28 Inclusive

Species, variety, and number	Percentage heads infected							
	1921	1922	1923	1925	1926	1927	1928	Av.
Triticum vulgare								
Glyndon Fife, Minn. 163	1	2	0	9	0	5	11	4.0
Kitchener, Minn. 2153	2	19	5	71	5	25	60	26.7
Kota, Minn. 2151	2	4	4	69	6	3	34	17.4
Marquis, Minn. 1239	7	33	7	65	9	6	28	22.1
Prelude, C. I. 4323	3	8	4	12	7	2	41	11.0
Prston, Minn. 924	T	7	3	44	4	17	6	11.6
Triticum durum								
Acme, Minn. 1967	8	32	4	76	9	35	90	36.3
Mindum, Minn. 470	12	26	3	33	12	16	73	25.0
Monad, Minn. 2156	11	38	10	91	7	43	81	40.1

TABLE III

Percentages of Fusarial Head and Seed Blight on Wheat Varieties and Hybrids at Waseca in 1923 and 1925, and at University Farm in 1923, 1925, and 1926

Hybrid or variety and number		Percentage of heads infected*							Percentage of seeds infected						
		Waseca			University Farm				Waseca			University Farm			
		'23	'25	Av.	'23	'25	'26	Av.	'23	'25	Av.	'23	'25	'26	Av.
Hybrids															
Marquis x Preston	II-15- 3†	9	7	8.0	3	22	12	12.3	1	1	1.0	T	7	5	4.0
	II-15- 5	18	11	14.5	6	35	20	20.3	2	3	2.5	1	10	7	6.0
	II-15- 6	16	8	12.0	11	35	13	19.6	2	2	2.0	1	8	4	4.3
	II-15- 7	15	14	14.5	4	29	9	14.0	2	4	3.0	T	4	5	3.0
	II-15- 8	16	5	10.5	6	18	15	13.0	1	1	1.0	1	2	6	3.0
	II-15-10	12	5	8.5	8	..	17	....	1	2	1.5	1	..	11	....
	II-15-11	9	2	5.5	2	15	7	8.0	1	1	1.0	T	3	3	2.0
	II-15-13	12	7	9.5	3	16	25	14.6	1	2	1.5	T	3	10	4.3
	II-15-16	13	4	8.5	6	28	20	18.0	1	1	1.0	1	5	7	4.3
	II-15-17	15	3	9.0	2	10	7	6.3	2	1	1.5	T	2	3	1.5
	II-15-19	13	8	10.5	6	33	15	18.0	1	1	1.0	T	6	6	4.0
	II-15-20	12	6	9.0	5	12	3	6.6	1	1	1.0	1	2	1	1.3
	II-15-21	7	6	6.5	4	35	9	16.0	1	1	1.0	T	4	3	2.3
	II-15-22	15	3	9.0	3	21	4	9.3	1	1	1.0	T	3	1	1.3
	II-15-23	8	2	5.0	2	13	1	5.3	1	1	1.0	T	2	T	0.7
	II-15-24	7	6	6.5	3	17	1	7.0	1	1	1.0	T	4	T	1.3
	II-15-25	6	3	4.5	1	11	5	5.6	1	T	1.0	0	1	2	1.0
	II-15-26	10	7	8.5	4	41	12	19.0	1	2	1.5	1	8	4	4.3
	II-15-28	15	3	9.0	2	8	4	4.6	2	1	1.5	T	1	1	0.7
	II-15-29	18	9	13.5	3	42	7	17.3	2	1	1.5	T	7	3	3.3
Marquis x Haynes Bluestem	II-15-31	5	2	3.5	0	6	1	2.3	0	1	0.5	0	T	T	T
	II-15-32	10	2	6.0	2	6	4	4.0	1	T	0.5	T	2	1	1.0
	II-15-34	11	1	6.0	2	27	7	12.0	1	T	0.5	T	5	1	2.0
	II-15-36	4	2	3.0	0	12	1	4.3	T	T	T	0	2	1	1.0
	II-15-39	8	5	6.5	1	21	3	8.3	1	1	1.0	T	3	1	1.3
	II-15-40	7	1	4.0	4	27	1	10.6	1	T	T	T	3	1	1.3
	II-15-41	16	3	9.5	1	19	1	7.0	2	1	1.5	T	3	T	1.0
	II-15-42	6	3	4.5	2	..	3	....	1	1	1.0	T	..	1	....
Marquis x Iumillo	II-15-43	15	3	9.0	6	48	12	22.0	2	1	1.5	1	14	6	7.0
	II-15-44	13	3	8.0	5	24	9	12.6	1	1	1.0	1	10	3	4.6
	II-15-59	14	T	7.0	11	24	6	13.6	1	2	1.5	1	6	6	4.3
	II-15-51	20	2	11.0	7	13	17	12.3	2	1	1.5	1	4	8	4.3
	II-15-55	16	5	10.5	9	28	12	16.3	1	2	1.5	1	15	8	8.0

TABLE III—*Continued*

Percentages of Fusarial Head and Seed Blight on Wheat Varieties and Hybrids at Waseca in 1923 and 1925, and at University Farm in 1923, 1925, and 1926

Hybrid or variety and number	Percentage of heads infected*							Percentage of seeds infected						
	Waseca			University Farm				Waseca			University Farm			
	'23	'25	Av.	'23	'25	'26	Av.	'23	'25	Av.	'23	'25	'26	Av.
Marquis x Kanred II-18- 8	9	7	8.0	4	34	4	14.0	1	1	1.0	0	11	2	4.3
II-18-57	12	2	7.0	1	40	8	16.3	1	T	0.5	T	13	2	5.0
II-18-58	12	2	7.0	1	74	4	26.3	1	T	0.5	T	9	1	3.3
II-B2- 5	14	8	11.0	3	33	4	13.3	2	1	1.5	T	10	1	3.6
II-B8-11	21	11	16.0	2	69	9	26.6	2	2	2.0	T	25	4	9.6
Triticum vulgare														
Glyndon Fife, Minn. 163 ..	6	2	4.0	0	9	0	3.0	T	T	T	0	2	0	1.0
Haynes Bluestem, Minn. 169	1	1	1.0	1	..	0	....	T	T	T	T	..	0	....
Kitchener, C. I. 2153	20	17	18.5	5	70	5	26.6	2	4	3.0	T	33	2	11.6
Kota, C. I. 5878	14	5	9.5	4	69	6	26.3	1	T	0.5	T	19	2	7.0
Kota x Marquis, N. D. 1656	..	5	....	..	69	..	....	..	12	....	..	19	..	....
Marquis, Minn. 1239	16	15	15.5	7	65	9	27.0	2	4	3.0	1	17	4	7.3
Marquis x Kota, N. D. 1658	..	..	....	..	60	..	....	..	..	....	..	18	..	....
Preston, Minn. 924	10	2	6.0	3	44	4	17.0	1	1	1.0	T	11	1	4.0
Prelude, C. I. 4323	1	..	....	4	12	7	7.6	1	..	....	T	6	3	3.0
Red Bobs, C. I. 2157	21	9	15	4	40	37	27.0	2	2	2.0	T	13	23	12.0
Ruby, C. I. 2153	5	4	4.5	3	18	14	11.6	1	1	1.0	T	..	6	....
Triticum durum														
Acme, C. I. 1967	34	11	22.5	4	76	9	29.6	5	2	3.5	1	26	23	16.6
Arnautka, C. I. 2103	10	5	7.5	4	15	..	....	1	1	1.0	1	1	..	....
Kubanka, C. I. 2194	26	15	20.5	5	46	..	....	3	4	3.5	1	22	..	....
Mindum, Minn. 470	8	4	6.0	3	33	12	16.0	1	1	1.0	T	13	4	5.6
Monad, C. I. 3320	23	17	20.0	10	91	7	36.0	2	4	3.0	2	31	4	12.3

* The percentages in the table for '23, '25, and '26 were reduced to the nearest whole number while figures in the text are based on calculations in which the percentages were carried out to the nearest tenth.

† Nursery stock numbers.

TABLE IV

Percentages of Head Blight in Wheat Varieties and Hybrids Grown in Duplicate Series at University Farm, St. Paul, Minnesota, in 1928

Variety and number	Percentage of heads infected		
	Series A	Series B	Average
Triticum vulgare			
Bobs, C. I. 4991	63	95	79
Ceres 1658, Minn. 2223	40	31	36
Chul, C. I. 2227	64	94	79
Converse, C. I. 4141	8	4	6
Erivan, C. I. 2397	66	66	66
Garnet, Minn. 2203	16	13	15
Glyndon, C. I. 2870	11	10	11
Haynes Bluestem, C. I. 2874	5	12	9
Hope, C. I. 8178	23	5	14
Humpback, C. I. 3690	10	10	10
Huron, C. I. 3315	2	6	4
Java, C. I. 4966	37	70	54
Kitchener, C. I. 4800	26	95	60
Kota, C. I. 5878	48	20	34
Lynn, C. I. 6346	18	10	14
Marquillo, Minn. 2202	40	25	33
Marquis, C. I. 3641	17	40	28
Parkers Marquis, Minn. 2222	20	23	22

TABLE IV—*Continued*

PERCENTAGES OF HEAD BLIGHT IN WHEAT VARIETIES AND HYBRIDS GROWN IN DUPLICATE SERIES AT UNIVERSITY FARM, ST. PAUL, MINNESOTA, IN 1928

Variety and number	Percentage of heads infected		
	Series A	Series B	Average
Prelude, C. I. 4323	31	51	41
Progress, Minn. 2225	16	5	11
Quality, Minn. 2207	94	92	93
Red Fife, C. I. 3329	6	40	23
Red Saskatchewan, Minn. 2193	73	82	77
Resaca, C. I. 6390	10	10	10
Reward, Minn. 2204	70	84	77
Ruby, C. I. 6047	42	20	31
Sonora, C. I. 3036	95	90	93
Stanley, C. I. 4796	12	10	11
Webster, C. I. 3780	16	27	22
White Federation, C. I. 4981	67	95	81
Hybrids			
Kota x Marquis, Minn. 2242	89	77	83
Kota x Marquis, Minn. 2245	95	77	87
Kota x Marquis, Minn. 2244	93	84	89
Kota x Marquis, Minn. 2224	83	80	82
Kota x Natural Cross, Minn. 2240	6	6	6
Kota x Ruby, Minn. 2235	27	18	22
Marquis x Kota 1656-85, Minn. 2298	91	66	79
Marquis x Kota 1656-85, Minn. 2238	84	81	83
Marquis x Kota 1656-85, Minn. 2236	89	72	81
Marquis x Kota 1656-85, Minn. 2237	74	15	45
Triticum durum			
Acme, C. I. 5284	88	93	90
Akrona, C. I. 6881	57	18	38
Arnautka, C. I. 1494	3	19	11
Buford, C. I. 5295	70	81	76
D-46	85	83	84
Golden Ball, C. I. 6227	94	92	93
Iumillo, C. I. 1736	67	30	49
Kahla, C. I. 5529	77	70	74
Kubanka, C. I. 1440	98	87	93
Kubanka, No. 8, C. I. 4063	96	94	95
Mahoudi, C. I. 4592	89	100	95
Marouani, C. I. 1593	91	76	84
Mindum, C. I. 5296	68	79	73
Monad, C. I. 3320	89	73	81
Nodak, C. I. 6519	65	66	66
Peliss, C. I. 1584	83	60	72
Pentad, C. I. 3322	81	33	57
Sineuska, C. I. 4010	100	92	96
Velvet Don, C. I. 2222	94	33	64
Unnamed varieties			
C. I. 3172	12	19	15
C. I. 3192	92	97	95
C. I. 3193	93	90	91
C. I. 3196	85	96	91
C. I. 3207	1	0	1
C. I. 3231	86	90	88
C. I. 4918	90	92	91
C. I. 4919	95	97	96
C. I. 5112	3	8	6
Triticum dicoccum			
Khapli, C. I. 4013	95	98	97

TABLE V

Correlation Between Reactions to Fusarial Head Blight of Wheat Varieties Grown at Different Places in the Same Year, at the Same Place in Different Years, and in Duplicate Series in the Same Year*

Species	Location and year of test	Head or seed infection correlated	No. of varities or selections compared	Correlation coefficient
Triticum vulgare				
	Waseca, 1923 and 1925	seed	41	+.65±.06
	Waseca, 1923 and 1925	head	41	+.52±.08
	University Farm, 1923 and 1925	seed	41	+.35±.09
	University Farm, 1923 and 1925	head	41	+.32±.07
	University Farm, 1923 and Waseca, 1923	seed	41	+.42±.08
	University Farm, 1925 and Waseca, 1925	seed	41	+.59±.04
	University Farm and Waseca (Average 1923 and 1925)	seed	41	+.60±.07
	University Farm, 1925 and 1926	seed	41	+.22±.10
	University Farm, 1925 and 1926	head	41	+.15±.10
	University Farm, 1925, Series A and B†	seed	41	+.38±.09
	University Farm, 1925, Series A and B†	head	41	+.19±.10
	University Farm, 1926 and 1927	head	71	+.02±.08
	University Farm, 1926 and 1927	seed	71	+.02±.08
Triticum durum				
	University Farm, 1926 and 1927	head	154	+.06±.05
	University Farm, 1926 and 1927	seed	154	+.05±.05
	University Farm, 1927, Series A and B†	head	116	+.66±.04
	University Farm, 1927, Series A and B	seed	116	+.62±.04

---

* Some of these calculations were made by Dr. G. Nilsson-Leissner, as a part of a study of disease resistance while an International Education Board Fellow at the University of Minnesota.

† Series B was sown two weeks later than Series A.

TABLE VI

SUMMARY OF CORRELATION COEFFICIENTS BETWEEN SEVERITY OF FUSARIAL HEAD AND SEED BLIGHT OF WHEAT

Species	Location and year of test	Extent of comparison	No. of varities or selections compared	Correlation coefficient
Triticum vulgare				
	Waseca, 1923 and 1925	Average for two years	41	+.91±.08
	University Farm, 1923, 1925, and 1926	Average for three years	41	+.87±.03
	University Farm, 1926 and 1927	Average for two years	71	+.92±.01
	University Farm, 1926 and 1927	Average for two years	154	+.86±.01
Triticum durum				
	University Farm, 1927, Series A and B	One year	116	+.87±.02

TABLE VII

CORRELATION BETWEEN AVERAGE PERCENTAGES OF BLIGHTED HEADS AND OF BLIGHTED SEEDS IN TWO REPLICATED PLOTS OF DURUM WHEATS GROWN AT UNIVERSITY FARM, MINNESOTA, IN 1927

Average percentage of seeds blighted

Average percentage of heads blighted	3	9	15	21	27	33	39	45	51	57	63	69	75	81	87	F
6	2															2
12		3														3
18	2	3	1													6
24		4	4													8
30	1	2	1													4
36		3	3	2												8
42			2	4												6
48			1	1	1											3
54				2	1	1										4
60			1	1	1	2	3									8
66				1	3	4		2								10
72				1	2		2	2	1	1		1				10
78						5	6				1					12
84						1	4	3	1	3	1	1	1			15
90						1	1	2	1	2	1		1			9
96									2	1	2	1	1		1	8
F	5	15	13	12	8	14	16	9	5	7	5	3	3	0	1	116

$r = +.866 \pm .016$

TABLE VIII

Correlation Between Average Percentages of Blighted Heads and of Blighted Seeds in Durum Wheats Grown at University Farm, St. Paul, Minnesota, in 1926 and 1927

Average percentage of seeds blighted

Average percentage of heads blighted	1.5	4.5	7.5	10.5	13.5	16.5	19.5	22.5	25.5	28.5	31.5	34.5	37.5	40.5	43.5	F
2.5	2															2
7.5	1	9														10
12.5		6	4	3												13
17.5		2	8	2		1										13
22.5		1	6	2	4	3	1									17
27.5			3	1	3	3	1		1							12
32.5				1	4	4	3	1		1						14
37.5					1	2	2	2	2	1	3	1				14
42.5			1		1	3	3	5	4	3	1	3				24
47.5					1		2	2	4		3	3		2		17
52.5									1	2		1	1	1	1	7
57.5								1	1		1			1		4
62.5											2	1	1			4
67.5										1					2	3
F	3	18	22	9	14	16	12	11	13	8	10	9	2	4	3	154

r=+.862±.014

TABLE IX

Effect of Date of Sowing on Development of Fusarial Head and Seed Blight of Wheat at University Farm, Minnesota

Year	Date of sowing	Variety	Percentage of heads infected	Percentage of seeds infected
1923	April 27	Average of 52 varieties	4.9	..
	May 4		3.1	..
	May 12		T+	..
1925	April 23	Marquis, Minn. 1239	13.5	5.0
	April 30		2.5	0.7
	May 6		1.5	0.7
	April 23	Monad, Minn. 2156	32.5	14.4
	April 30		1.0	0.5
	May 6		0.5	0.3
	April 25	Average of 41 varieties	29.6	5.1
	May 8		7.4	2.2
1926	April 22	Average of 50 varieties	8.3	3.9
	May 4		T	T
1927	April 29	Marquis, Minn. 1239	5.7	2.5
	May 6		100.0	51.5
	May 13		86.7	43.8
	April 29	Monad, Minn. 2156	43.0	31.8
	May 6		100.0	80.0
	May 13		96.5	37.5

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CONTENTS

Page

The problem 5
- Enormous area of aspen lands 5
- Agricultural development slow 5
- Present limited use of aspen 6
- Will consumption keep pace with potential production? 7
- Natural conversion to pine or spruce 7
- Can aspen lands be made more valuable? 8

History of the aspen forest 9
- Result of cutting and fires in original forests 9
  - Origin of pure stands of aspen 10
  - Origin of mixed stands of aspen and conifers 10

Description of the aspen forest 11
- Species of aspen and their ranges 11
- Associated species 12
- Occurrence of aspen 13
- Sites 14
- Composition of the stand 21

Growth and yield 23
- Well stocked stands 23
- Understocked stands 27
- Overstocked stands 30

Maturity, rotation, and longevity 31
- Influence of decay in forest management of aspen 32

Reproduction of aspen 33
- Seedlings 34
- Suckers 34

Management of pure aspen as a permanent crop 36

Natural conversion of aspen to conifers 38
- Advance growth in original coniferous stands 40
- Source and supply of coniferous seed 40
  - Seed trees 41
- Effect of rodents and other forms of animal life on establishment of conifers 43
- Effect of fire in preventing establishment of conifers 46
- The aspen forest floor 46
- Effect of shading and competition with other vegetation 47
- Growth of conifers in aspen stands 49
  - Height growth 50
  - Diameter growth 52
  - Volume growth 52
  - Relation of growth of conifers to that of aspen 55
- Development of conifers and final outcome 56

Man's assistance in the conversion process 57
- Fire protection 57

Cuttings in mature aspen 57
    Effect on associated conifers 58
Release cuttings 60
Disturbing the forest floor 61
Sowing seed 62
Planting in the aspen type 63
    Favorable and unfavorable conditions for planting 64
    Planting practice 65
Results in plantations on aspen lands 67
Costs of planting 67

Advantages of aspen and coniferous stands 68

Summary 69

Literature cited 71

Appendix 75
Volume tables for aspen and paper birch 76
Common names and scientific names of trees mentioned in the text 83
Common names and scientific names of shrubs and herbaceous vegetation mentioned in the text 83

ILLUSTRATIONS

Page

Fig. 1. Aspen–paper birch land approximately five years after fire "brush," St. Louis County, Minn. 11

2. Areas on which aspen predominates 13

3. Site index curves for aspen 15

4. Well stocked aspen 40 years old 24

5. Stems of two aspen suckers 35

6. Natural conversion of aspen-birch to balsam fir, St. Louis County, Minn. 39

7. Natural conversion of aspen to Norway and white pine, Oneida County, Wisc. 39

8. Aspen stand with large white pine seed tree, Chippewa National Forest, Minnesota 42

9. White pine damaged by snow-shoe rabbits 45

10. Natural conversion of birch to spruce under forest management in Finland 59

The first season's field work in Minnesota, resulting in the collection of data on 83 plots, was done by E. E. Probstfield, with the help of student assistants, G. E. Sargent and F. G. Whitney. E. T. Erickson and F. G. Whitney assisted in the second season. The Wisconsin Conservation Commission and its field personnel in northwestern Wisconsin, particularly Rangers Henry Freund and Ray Hassett, rendered valuable assistance. L. M. Wood assisted in the analysis of the data. Raphael Zon, Director of the Lake States Forest Experiment Station, was a never-failing source of encouragement and inspiration. To all these, the authors wish to express their grateful acknowledgment.

FOREST POSSIBILITIES OF ASPEN LANDS IN THE LAKE STATES

Joseph Kittredge, Jr., and S. R. Gevorkiantz

THE PROBLEM

Enormous Area of Aspen Lands

The most characteristic sight in traveling through northern Minnesota and Wisconsin is the monotonous and scrubby looking growth of small aspen trees. Actual surveys indicate that the aspen, often somewhat mixed with paper birch, is the most abundant and wide-spread type of forest vegetation in the northern Lake States. In St. Louis County, Minnesota, Hansen (1923) found that it occupied 70 per cent of the cut-over land. In northern Wisconsin the soil types on which aspen grows abundantly represent more than 50 per cent of the total forest area. In Menominee County, Michigan, the Land Economic Survey finds 34 per cent of the forest area in aspen. Even in the northern part of the Lower Peninsula of Michigan, which is usually thought of as a region of jack pine and scrub oak, the Survey figures indicate one third of the area in aspen. The extensive field work in this study of aspen, chiefly in northern Minnesota and northwestern Wisconsin, led to estimates, confirmed by the figures cited, that the aspen lands in northern Michigan occupy about one third and in northern Wisconsin and Minnesota almost two thirds of the total forest area. This represents a land area of about 21 million acres. The enormous size of this area in itself constitutes a major problem of land use.

Agricultural Development Slow

Improved farm land in the northern part of the Lake States increased from 1910 to 1924 at the rate of about 250,000 acres a year. Considering that clearing and settlement are advancing northward, where climatic and economic conditions for farming are progressively less favorable, and that many of the settlers who have tried to make a living on these northern areas have been disillusioned; and, furthermore, that the importance of growing timber crops on large areas of these lands is being recognized, it seems unlikely that the rate of settlement will increase for some time in the future. Considerable portions of the land on which aspen grows are suitable for farming after they are cleared. On the assumption that the proportion of increase in improved farm land of the aspen type will correspond to the proportion that type is of the whole area of forest land (60 per cent), the rate of clearing is not likely to exceed 150,000 acres a year. At this rate, the clearing of 21 million acres of aspen lands would require about 140 years. Even if taken up at a more rapid rate, the area that will remain in aspen is enormous.

Altho aspen is characteristic of fertile soils, large areas of the aspen type, owing to their rough and rocky character, will never be suitable for farming. The largest single area of this kind is the triangular region north of Lake Superior, in Minnesota. A large part of the 21 million acres, therefore, may be expected to produce at least one and probably two or three crops of aspen before it will be needed for agriculture.

Present Limited Use of Aspen

The use of aspen in the region where it grows or to which it can be shipped profitably is extremely small in comparison with the amount that is or soon will be available. The census (1927) of 1926 reported only 33,000 cords used for pulpwood. Possibly 15 million board feet are used annually for excelsior and lumber. Crocker (1926) estimated the consumption of aspen in 1925 as 173,000 cords in the three Lake States. An unknown amount, which may easily amount to 50,000 or 100,000 cords, is used by settlers for firewood and poles. The total present yearly consumption of aspen in the Lake States is estimated, therefore, to be between 175,000 and 250,000 cords.

Aspen is used chiefly for paper pulp, excelsior, boxes, heading, pails, staves, lumber, and fuel. In Europe and also in Japan it is extensively used and highly valued for matches. This use may develop gradually in this country also. Similarly, the utilization for excelsior, box boards, and lumber may increase, altho there is no immediate prospect of a rapid increase. For paper pulp, aspen reduces readily by the sulphite or the soda process and yields pulp of excellent color, that bleaches easily (Wells and Rue, 1927). Actually, little aspen is being used in the sulphite process. Considering the concentration of paper mills in the Lake States, particularly in eastern Wisconsin, and the diminishing supplies of spruce, balsam fir, and hemlock, consumption of aspen for paper pulp may increase considerably. This increase, however, will not come immediately (1) because much hemlock will be available for the next 10 years from the lumbering operations of northern Wisconsin and Michigan, and (2) because the use of large proportions of apsen will require costly modifications in the manufacturing processes at most of the existing paper mills. The present limited use of aspen, therefore, is likely to continue without marked change for another 10 years, after which its consumption may be expected to rise at an accelerating rate.

Will Consumption Keep Pace with Potential Production?

If the present consumption of aspen is about 200,000 cords a year and probably will not exceed 250,000 in the next 10 years, how do these figures compare with the amount of aspen already available or that will become merchantable in 10 to 20 years? The stand of aspen in the Lake States in 1928 may be estimated at 30 million cords. At a rate of consumption of 250,000 cords a year, this is enough for more than 100 years. These 30 million cords represent the stand on about 4 million acres. There remain 17 million acres of small growth, much of it well stocked, that is growing at the rate of about one sixth of a cord per acre per year. The amount of aspen, therefore, is increasing a little less than 3 million cords a year. In 20 or 30 years the annual growth will probably double, or become 6 million cords. The growth each year at these rates will supply the present demand for 12 to 24 years. Even if the estimates of area, stand, and growth are high, the conclusion is still unquestionable—that consumption of aspen is not keeping pace with the growth. Moreover, there is little prospect that the growth will be utilized for many years. Agricultural development will require only a fraction of the aspen lands. What then, is to be done with these millions of acres to obtain the best use and highest value from them?

Natural Conversion to Pine or Spruce

A desirable solution of the problem of the use of the aspen lands would be the replacement of aspen by other more valuable species, as spruce or pine. The process is going on naturally and slowly over limited areas. Observations lead to the estimate that not more than 20 per cent of the aspen land in the northern Great Lakes region as a whole has an appreciable representation of more valuable tree species coming up with or under the aspen. This estimate is confirmed by figures from the survey of St. Louis County, Minnesota, by Hansen (1923), in which he found 24 per cent of the cut-over area, most of which was aspen and paper birch, to contain from 10 to 60 per cent of conifers in mixture. St. Louis County forms a part of northeastern Minnesota, where the conifers, particularly balsam fir, are most commonly represented in the aspen stands. The estimates in the field study for this section placed the percentage of aspen with a mixture of conifers at 30. The greater proportion of conifers in this region, however, is counterbalanced by the wide areas in other parts of Minnesota and Wisconsin where they are not found on aspen lands.

Moreover, the areas on which spruce, pine, or other conifers are found with aspen are increasing slowly, perhaps even decreasing. The slow increase is due (1) to the fact that logging and fires have left only occasional and scattered trees of pine or spruce from which seed might blow to reseed the aspen lands. (2) The limited supply of seed from the few scattered seed trees is not more than enough to feed the many hungry squirrels, mice, and other rodents, which devour most of it before it germinates. (3) The seeds are carried only limited distances from the seed trees and when the trees are few and far between they reseed only a small part of the total area. These are ample reasons why the reseeding of aspen lands to conifers is progressing slowly. To make matters worse, large areas of aspen lands burn over in the frequent bad fire seasons. A fire is almost certain to kill all the young conifers in its path. While the effectiveness of efforts to protect the forest lands from fire is increasing, the area burned annually, which amounted to 381,000 acres on the average in the years from 1916 to 1925, may easily account for the destruction of small conifers on a larger area of aspen land than was reseeded in the same time. As fire protection improves, the rate of natural conversion to pine and spruce will undoubtedly increase, but the progress will be slow for at least 50 years. After that many of the present small pines and spruces or those that will become established in the next few years will reach seed-bearing age and will in turn scatter seed to convert additional areas to more valuable kinds of forest.

Can Aspen Lands Be Made More Valuable?

There is little prospect that aspen by itself will soon become more valuable. At present, it is worth little or nothing except on areas near a manufacturing plant that uses aspen. Similiarly, the oversupply for several years promises to be valuable only on the areas favorably located with respect to markets. White and Norway pine, however, are now worth $8.00 to $12 a thousand board feet, and white and black spruce, $3.00 to $5.00 a cord. Balsam fir is less valuable, altho it is much used for pulpwood and lath. The demand for spruce and pine is generally strong and is increasing as the supply is decreasing. There is every reason to believe, therefore, that the pines and spruces will become more valuable. If the aspen lands can be made to produce spruce or pine, the conversion will almost certainly increase the value of those lands, even if the future values of pine and spruce should not be higher than the present.

The conifers do not reach merchantable size as soon as the aspen, but their greater value may more than offset the greater cost of growing them. It may also pay the cost of conversion by planting seedlings of spruce or pine and raising them to maturity.

Certain questions may well be asked by those who own or are interested in the northern cut-over lands where aspen is so common. How much will aspen yield at different ages? At what ages or sizes should it be cut? Does it pay to grow aspen? Is the aspen being replaced naturally by more desirable species? Can the conversion be hastened by silvicultural treatment? If not, can it be accomplished by seeding or planting? Under what conditions will the conversion of aspen to pine or spruce pay?

In an attempt to answer these questions, 305 areas were examined carefully in 1925 and 1926, chiefly in Minnesota and northwestern Wisconsin. On 123 areas data were taken to show the growth and yield of well stocked aspen; on 17, the growth of paper birch; and on 165 the natural conversion of aspen-birch to conifers. Seven hundred and seven aspen trees were cut and analyzed as the basis for volume tables already published (Cloquet, 1926). One hundred and sixteen paper birch trees were analyzed and from the measurements the volume tables for paper birch in the appendix were prepared. The answers that will be suggested to the foregoing questions should be applicable to conditions in northern Minnesota, northern Wisconsin, and probably also in both parts of northern Michigan.

HISTORY OF THE ASPEN FOREST

The uplands of the northern Lake States region were originally forested chiefly with pine, spruce, balsam fir, hardwoods, and hemlock. Aspen occurred either in small patches where fires had burned, or as scattered trees in the old-growth forest.

It formed merely an inconspicuous part of the brush in the forest. However, careful inspection of all tree species in the remaining old-growth forests usually reveals aspens. It was found in 3 of the 10 pine stands counted by Morbeck (1922) in northern Minnesota. It forms an understory in places in the old white pine forest of the Chippewa National Forest, as mentioned by Truax (1915) and observed by others. From one to 35 per cent of "poplar," doubtless mostly aspen, was found in the white spruce areas by Kenety (1917). It is a frequent constituent, altho an inconspicuous and unimportant one, in the northern hardwood-hemlock forests, as shown by Frothingham (1915). Aspen was, therefore, widely distributed in the northern Lake States before logging began. The thousands of acres of aspen in nearly pure stands, which are so characteristic of the region now, have developed almost entirely within the last 70 years.

Result of Cutting and Fires in Original Forests

In the early days of logging in the old-growth pine forests, only the largest and best trees were cut. Gradually, as the value of lumber increased, smaller and poorer pines were taken. As the stands of white pine became harder to find, the best of the white pine was culled from the mixtures of white and Norway pine and of white pine and hardwood-hemlock. More recently, Norway pine and hardwood-hemlock became valuable and heavy cuttings removed all the trees down to 10 or 12 inches in diameter. A large proportion of the smaller trees that were left was destroyed or damaged in logging. The white pine forests that had been cut lightly for the best trees were gone over again, and most of the remaining timber was removed. In the process, most of the small aspens were cut off or broken.

Aspen stumps do not sprout, but the wide-spreading roots give rise to new stems, called suckers. Fires have the same effect as cutting.

Origin of Pure Stands of Aspen

Fires that burned through the old pine slashings destroyed all living trees in their path, with the occasional exception of a big thick-barked pine. The small pines, spruces, balsam firs, and aspens were destroyed. The pines and spruces did not sprout but the aspen suckers came up promptly and vigorously and were many times more numerous than were the aspen trees in the old stands.

Much of the cut-over land burned several times within the 10 or 20 years following cutting. The repeated fires even more completely destroyed existing trees (Fig. 1). After every fire, however, aspen suckers came up more abundantly and more extensively. Seedling aspens, on the contrary, are rare because few aspen seed trees were left, and conditions were generally unfavorable to germination and establishment. The present large area of nearly pure stands of aspen is due largely to its ability to produce many suckers from the roots for every tree that is killed by logging or fire.

Origin of Mixed Stands of Aspen and Conifers

White pine, spruce, or balsam fir seedlings were usually on the ground as advance growth under the old stands. More than 21,500 white pine seedlings to the acre were found in a stand of old-growth white pine in northwestern Wisconsin. In northern Minnesota, Morbeck (1922) found from 1,300 to 16,000 white pine seedlings to the acre under old-growth white pine stands. Cutting destroyed only part of this young growth. Fires destroyed all of it wherever they burned. Occasional areas and patches, however, escaped the fires and on these areas the pines and spruces left after logging have lived and grown. The aspen came up from suckers after cutting on the same areas and, as its early growth is much more rapid, the aspen has usually formed an overstory with pine, balsam fir, and spruce as an understory. In this way a considerable part of the larger conifers in mixture with the aspen originated.

Some defective or small trees of pine, balsam fir, and spruce were left in the early logging. Those that survived produced seed, the result being scattered seedlings and irregular patches under the aspen on some of the burned-over areas. Wind storms and repeated fires, however, have destroyed much of this source of coniferous seed in most parts of the region. On the whole, mixed stands of aspen and conifers are not common or extensive.

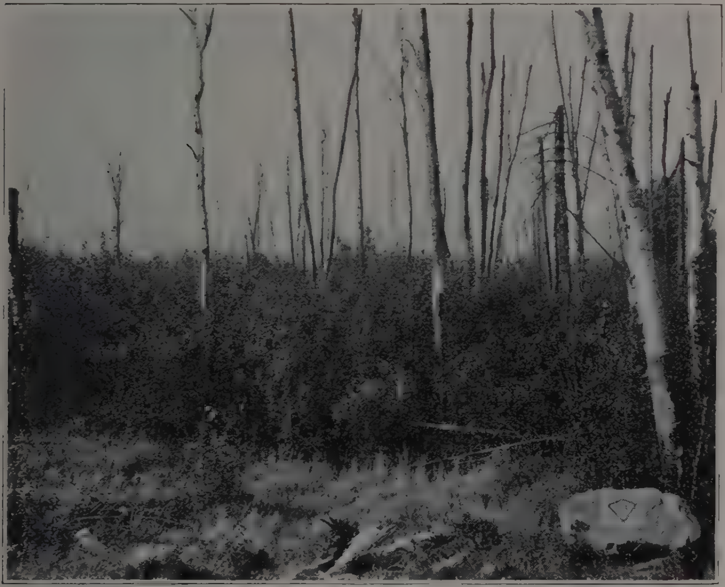

Fig. 1. Aspen-Paper Birch Land Approximately Five Years After Fire "Brush." St. Louis County, Minn.

DESCRIPTION OF THE ASPEN FOREST

Species of Aspen and Their Ranges

The species that makes up the bulk of the aspen forest in the northern Lake States is the true aspen *(Populus tremuloides)*, commonly known as popple. It grows from Labrador to Hudson Bay and Alaska, throughout the Lake States, and as far south as Illinois and northern Missouri. Sometimes mixed with the aspen but much more often in separate patches, the large-tooth aspen *(Populus grandidentata)* is found, altho much less commonly, throughout the region except in southwestern Minnesota. A third species is the balsam poplar *(Populus balsamifera)*, sometimes called poplar or Balm-of-Gilead, which is also found in the northern half of Minnesota, Wisconsin, and Michigan. The aspen is much the most abundant of the three species and altho they have many similarities of habit, the material presented in this report will refer to the true aspen unless otherwise specified.

Associated Species

Altho most of the aspen forest appears to be wholly or predominantly aspen, other species occur commonly in mixture with and usually subordinate to it. Paper birch,[1] often called white birch, is the most common and most conspicuous of the associated species. Over small areas or in patches the birch may outnumber the aspen or even occur in pure stands. This is frequently true around lake shores, where, it has been suggested, the predominance of birch may be due to the harvesting of the aspen by beavers. The largest aggregate area where paper birch predominates is the strip of land draining into Lake Superior along its north shore, in Minnesota. Elsewhere and more commonly birch is found mixed with aspen as a more or less suppressed understory of small, poorly developed birches, which may be even more numerous than the aspens. The suppressed birches are usually as old as the aspens and have persisted, altho unable to keep pace with its rapid height growth during the first few years. Seedlings or young saplings of paper birch are rarely found under older aspens, except one-year-old seedlings, which sometimes start abundantly on rotten wood but rarely survive.

Other species associated with aspen in the order of their abundance are balsam fir, white pine, white spruce, black spruce, sugar maple, red maple, Norway pine, jack pine, elm, red oak, bur oak, black ash, green ash, yellow birch, basswood, jack oak, pin cherry, ironwood, and tamarack. Of these, only balsam fir, pine, spruce, and sugar maple are sufficiently numerous to have any importance. Jack and Norway pine are found with aspen only where there are openings in which they have been able to maintain themselves, and on the drier, sandier soils. The other species form more or less important parts of an understory on areas where fires have not burned repeatedly. The larger trees were present as advance growth or germinated from seed scattered shortly after the aspen started. Balsam fir is the only one that has aggressively seeded under the aspen stands. White pine and the spruces have also seeded in to a limited extent, but ordinarily only small seedlings are to be found.

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[1] The scientific names of trees and plants mentioned in the text will be found in the appendix.

Occurrence of Aspen

Aspen grows on a wide variety of soils, in fact, on almost any of the soils in the northern part of the region except the driest and sandiest, which are occupied by jack pine. Figure 2 shows the general areas in which aspen predominates in Minnesota and Wisconsin. Ordinarily, it is not found in the swamps on peat soils, altho one area was measured on which the aspen was growing well on peat more than 5 feet deep. If the soils are grouped according to the surface geological formation, aspen is found on all except the coarser sands of glacial outwash and the shallowest soils of the rock outcrops. It grows abundantly on sandy moraines, clay moraines, till, both sandy and clayey lake-wash till, and lake-bed clays. It was found most commonly in this study on sandy moraines and on till. If the soils are grouped according to texture, aspen was found on sands that are well supplied with moisture or underlaid not too deeply by a layer of finer soil, on fine sands, sandy loams, fine sandy loams, silt loams, clay loams, and even clay along the south shore of Lake Superior—most commonly on sandy loams and fine sandy loams.

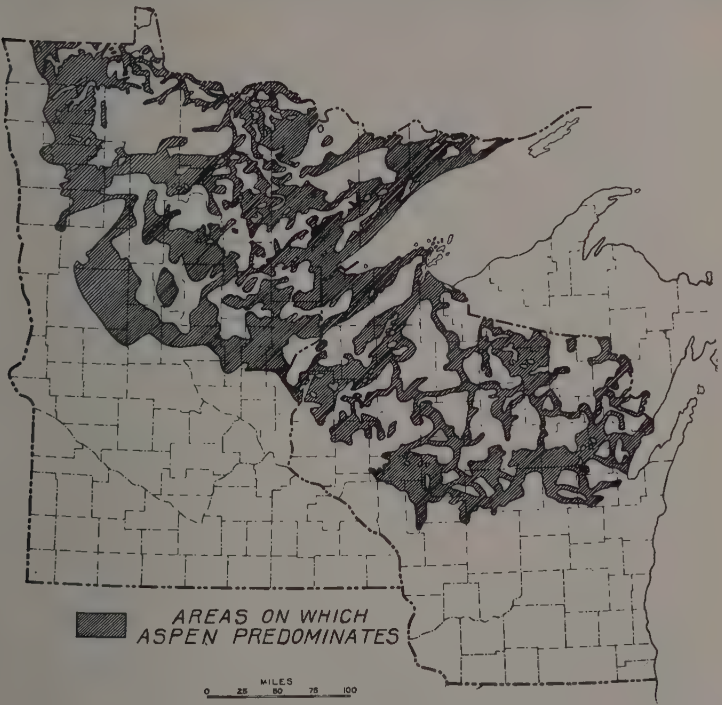

Fig. 2. Areas on Which Aspen Predominates

A species that thrives on such widely differing soils is evidently not exacting in its requirements. The only soil limitation is found in the deep, medium, or coarse sandy soils, which are least retentive of moisture and low in their content of nitrogen, lime, and other nutrients. These sandy soils are characterized by less than 10 per cent of silt and clay, less than 0.03 per cent of nitrogen, less than 0.2 per cent of lime, and a minimum moisture content for the existence of plants,[2] about 2 per cent or less. Organic matter may be as low as one per cent. Acidity may vary from extremely acid, with a pH as low as 4.3, to slightly acid or neutral, with pH 7.

Sites

The rate of growth and the yield of aspen at any given age vary with the productivity of the soil or, as it is more commonly known in forestry, with the quality of site. Site quality may be defined and indicated in several ways. The most satisfactory, based upon the aspen forest itself, is the arbitrary classification of the stands by a numerical value for what is called the site index. This is simply the average total height of the dominant trees in a stand at 50 years old, or the height that the average dominant tree in a younger or older stand would have at 50 years. The dominant trees are those whose crowns extend above the general level of the forest canopy and receive full light from above and partial light from the side. They are larger than the average trees in the stand and have well developed crowns. Altho the crowns may be crowded on the sides, these trees have had ample space to develop as compared to other trees in the stand. For the determination of site index, moreover, they should be trees whose height growth has not been affected by cuttings, fire, or damage of any kind. The curves in Figure 3 represent the site indexes for aspen at different ages.

In order to determine the site index for a given stand, it is necessary to average the heights of at least 5 and preferably more dominant trees on each acre. For example, in a 30-year-old stand, 5 dominant trees are found to be 35, 38, 40, 36, and 32 feet high. The average dominant height is, therefore, 36 feet (Fig. 3). By following perpendicularly along the line from 30 on the scale of age until it crosses the horizontal line from 36 on the scale of height of average dominant tree, the intersection comes about one-tenth of the distance below the curve of 50 toward the curve of 40. The difference between 50 and 40 is 10, and one-tenth of this is one, so the site index for this 30-year-old stand with an average dominant height of 36 feet is 50 minus one, or 49 feet. The site index of any stand may be obtained in the same way.

These site indexes correspond with what is known of the productivity of the different soils on which aspen grows. For example, the medium to coarse sandy soils of outwash plains or sandy moraines, which are drouthy and low in nutrients, usually have site indexes below 55, except where the soil is close to swamp or ground water level. The fine sandy soils of outwash plains, the clay and clay loam soils around the shores of Lake Superior, and the shallow sandy loam soils on the rock outcrops in northeastern Minnesota belong also to site index classes less than 55. The site index classes above 67 include the silt loam soils, except those shallowly underlaid by rock; the fine sandy loam soils on bowlder clay or clayey moraine or on the heavier soils of old lake beds and those not too shallowly underlain by rock; and the fine sandy soils on bowlder clay. The other groups of soils on which aspen was found are in the intermediate site index classes, between 55 and 67.

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[2] Technically this is known as the hygroscopic coefficient.

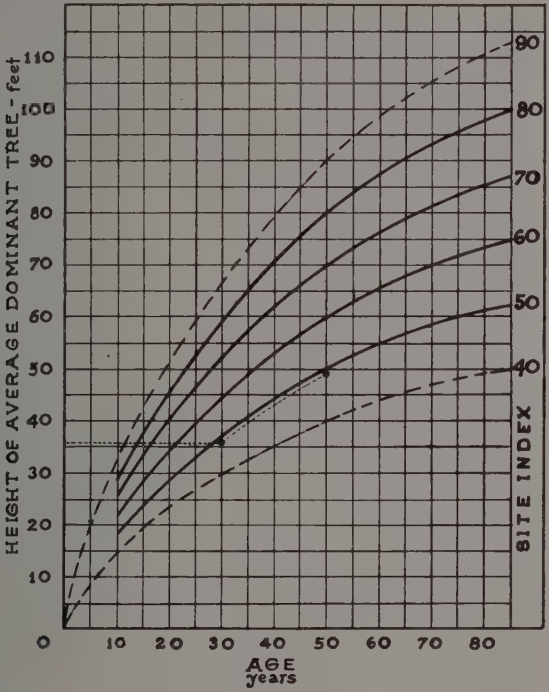

Fig. 3. Site Index Curves for Aspen

A general statement of the geographical distribution of the good and poor sites is impossible, because the glacial soils of the region, and hence the sites, are inextricably intermingled within short distances. Certain large areas with predominantly good and poor sites for aspen may be mentioned. Poor sites, with indexes less than 55, are characteristic of the hilly, gravelly moraines that occupy a large area in Vilas and Oneida Counties, in north central Wisconsin, and a strip of similar topography from Aitkin through Cloquet and northeastward into Lake County, in Minnesota. The red clays and clay loams along Lake Superior, chiefly on the Wisconsin shore from Superior to Port Wing and south of Washburn and Ashland, are also poor sites; the areas of loam and silt loam soils of northwestern Itasca County and of Beltrami County southeast of Red Lake, in Minnesota, are excellent sites with indexes generally above 67.

Another means of judging the fertility of the soil and of checking the site index for aspen is the brush and ground cover under the aspen. Many kinds grow commonly on all soils on which aspen is found; others are limited to certain site index classes. Mountain maple, dogwood, alder, clintonia, pyrola, arbutus, raspberry, bedstraw, starflower, baneberry, clubmoss (except ground pine), ferns (except brake), hepatica, meadow rue, Canada mayflower, choke cherry, viburnum, bellwort, dwarf raspberry, wild ginger, currant or gooseberry, mitrewort, and twisted stalk, usually indicate site indexes of 53 or higher. Sweet fern indicates a site index of less than 47. Blueberry, ground pine, and wintergreen indicate site indexes less than 60.

The associated tree species also give a check on the site indexes. Ash, hop-hornbeam, northern white cedar, balsam poplar, bur oak, and basswood are found chiefly on sites with indexes above 57. Yellow birch and elm usually occur on those with indexes above 60. Black spruce and Norway pine rarely occur on sites with indexes higher than 64, and scarlet and jack oak are usually on those with indexes less than 55.

In estimating the growth of stands of aspen, the correct determination of the site index, or quality of site, is important. It is worth while to estimate the site quality by all three of the ways suggested and to check one against the other, because sometimes the relation between the average height of the dominant trees and their age, alone, may not be a reliable index. Altho neither the vegetation nor the soil alone can be relied upon for an accurate appraisal of site quality, the combination of the two may be more reliable than the site index figure alone. For example, on one plot the average height of dominant trees was 35 feet at 34 years of age, which corresponded to a site index of 44. Viburnum, clintonia, wild ginger, twisted stalk, and bedstraw indicated a site equivalent at least to that represented by site index 55. On the other hand, blueberry indicated that the index was unlikely to be more than 58. The soil corresponded to that of site index 58. In this case, the low height was probably due to the fact that the aspens had been more or less suppressed by old-growth pines, which were cut 5 years previously. The soil and plant indicators checked one another and made possible the correction of a site index figure that was seriously low.

The site index classification is used for the division of the aspen growth and yield figures according to the productivity of the sites. Five 10-foot site index classes cover the range of sites on which aspen was found growing. These classes, beginning with the best, are 80, 70, 60, 50, and 40. By far the larger proportion of the aspen stands is found in classes 70, 60, and 50. Class 60 contained the largest number of the measured plots and undoubtedly includes the average for the region as a whole. It is sometimes difficult to think of the productivity of the soil or the quality of site in terms of these site indexes. It may be helpful, therefore, to remember that site index 60 indicates a site of average quality, 70 and over one of good quality, and 50 and under one of poor quality.

As there are large differences in the yields of aspen on the different sites, it is important to know not only the site index for a specific stand but also what proportion of the aspen type is growing on the poorer sites, on which it may never reach merchantable size. A classification into corresponding site indexes of the surface formations on which aspen was found by Hansen (1923) showed that in St. Louis County, Minnesota, about 20 per cent of the aspen is growing on sites of index less than 55. Twenty-two per cent of the well stocked plots in this study were found in classes 40 and 50. This percentage is probably high, because in selecting plots for the yield tables an attempt was made to obtain as many as possible of those representing both the extremely low and the extremely high site indexes, which occur less commonly and are harder to find than those of average quality. Of the plots selected to illustrate the development of conifers with the aspen and that were chosen without respect to density or site quality, 17 per cent were on site indexes less than 55. It is likely, therefore, that between 15 and 20 per cent of the aspen in the northern part of the Lake States occupies the poorer sites, represented by site indexes less than 55.

These quality classes, which are most easily recognized by the site indexes, or the relation between height and age of the dominant trees, are also distinct for well stocked stands in respect to the other factors measured in determining the volume and growth of forests. With occasional exceptions, the higher the site index for stands of the same age, the higher are the other factors, namely, basal area of stand, volume, average height, average diameter, and average annual growth per acre. The only factor that does not increase as the site index increases is the number of trees per acre. As the site index increases the number of trees per acre decreases, because the trees on the better sites grow larger and can not stand so close as the smaller trees on the poorer sites. These relationships become clearer by reference to Tables I, II, and III.

TABLE I

Yield Table of Well Stocked Aspen in Trees One Inch and Over in Diameter at Breast Height

Total cubic feet

Age	Av. total height of dominant trees	Av. height of trees	Av. diameter at breast height	No. of trees per acre	Basal area per acre	Total peeled volume per acre	Av. annual growth	No. of plots
years	feet	feet	inches		sq. ft.	cu. ft.	cu. ft.	
			Site index 80 feet at 50 years					
20	46	36	3.3	1,490	88	1,540	77	—
30	59	50	4.8	880	110	2,550	85	1
40	71	62	6.3	600	129	3,650	91	—
50	80	74	8.1	400	143	4,720	94	1
60	87	84	10.3	265	153	5,620	94	—
70	93	91	12.6	185	161	6,290	90	—
80	98	96	14.3	148	165	6,780	85	—
								2
			Site index 70 feet at 50 years					
20	40	34	2.9	1,800	83	1,340	67	7
30	51	46	4.2	1,065	102	2,180	73	5
40	62	57	5.4	760	120	3,160	79	4
50	70	68	7.0	495	133	4,060	81	2
60	76	76	9.0	330	144	4.840	80	3
70	82	82	10.9	235	151	5,420	77	3
80	86	86	12.6	180	155	5,750	72	1
								25
			Site index 60 feet at 50 years					
20	34	29	2.5	2,300	76	1,080	54	6
30	44	40	3.5	1,400	94	1,760	59	17
40	53	49	4.5	980	110	2,450	61	8
50	60	58	5.9	645	122	3,220	64	12
60	66	65	7.6	422	133	3,820	64	13
70	70	70	9.3	295	139	4,290	61	—
80	74	74	10.6	234	143	4,600	57	—
								56
			Site index 50 feet at 50 years					
20	29	23	1.9	3.200	60	710	36	5
30	37	32	2.7	1,910	75	1,170	39	4
40	44	39	3.5	1,300	88	1,620	41	4
50	50	47	4.6	856	98	2,140	43	4
60	55	52	5.8	580	105	2,520	42	3
70	59	57	7.1	400	109	2,820	42	—
								20
			Site index 40 feet at 50 years					
20	23	19	1.3	4.100	38	360	18	—
30	29	27	1.9	2.420	46	600	20	1
40	35	33	2.4	1,660	54	850	21	2
50	40	39	3.2	1,110	60	1,100	22	—

TABLE II

Yield Table of Well Stocked Aspen in Trees 6 Inches and Over in Diameter at Breast Height

Board feet (International Rule, ⅛ inch kerf.*)

Age	Av. total height of dominant trees	Av. height of trees	Av. diameter at breast height	No. of trees per acre	Basal area per acre	Volume per acre	Av. annual growth	No. of plots
years	feet	feet	inches		sq. ft.	bd. ft.	bd. ft.	
			Site index 80 feet at 50 years					
30	59	64	6.4	228	50	5,700	190	1
40	71	68	7.0	365	101	12,800	320	—
50	80	74	8.3	369	138	21,200	423	1
60	87	84	10.3	265	153	30,000	500	—
70	93	91	12.6	185	161	37,500	535	—
80	98	96	14.3	148	165	41,800	522	—
								2
			Site index 70 feet at 50 years					
30	51	63	6.0	170	33	3,800	126	5
40	62	66	6.7	319	80	9,200	230	4
50	70	70	7.6	403	124	16,700	334	2
60	76	76	9.0	320	143	23,700	395	3
70	82	82	10.9	235	151	30,100	430	3
80	86	86	12.6	180	155	34,800	435	1
								18
			Site index 60 feet at 50 years					
30	44	59	6.1	80	14	1,400	47	17
40	53	60	6.3	215	45	5,000	125	8
50	60	62	6.9	358	96	10.700	214	12
60	66	66	7.9	378	127	16,500	275	13
70	70	70	9.3	290	138	21,300	304	—
80	74	74	10.6	234	143	24,800	310	—
								50
			Site index 50 feet at 50 years					
40	44	53	6.1	74	13	1,400	35	4
50	50	54	6.4	200	42	4,500	90	4
60	55	55	7.0	306	81	8,200	136	3
70	59	59	7.6	327	102	11,500	164	—
								11

* Stump height, one foot; top diameter inside of bark, 5 inches. Bark is not included in volume.

TABLE III

Yield Table of Well Stocked Aspen in Trees 7 Inches and Over in Diameter at Breast Height

Board feet (Scribner Decimal C Rule*)

Age	Av. total height of dominant trees	Av. height of trees	Av. diameter at breast height	No. of trees per acre	Basal area per acre	Volume per acre	Av. annual growth	No. of plots
years	feet	feet	inches		sq. ft.	bd. ft.	bd. ft.	
			Site index 80 feet at 50 years					
30	59	70	7.5	79	24	1,400	46	1
40	71	73	7.9	216	74	5,700	142	—
50	80	77	8.7	304	124	14,200	284	1
60	87	84	10.4	255	149	23,300	388	—
70	93	91	12.6	185	161	29,900	426	—
80	98	96	14.3	148	165	32,900	411	—
								2
			Site index 70 feet at 50 years					
30	51	69	7.3	35	10	500	17	5
40	62	70	7.6	167	52	3,400	84	4
50	70	72	8.1	297	105	9,600	192	2
60	76	77	9.3	290	137	17,300	288	3
70	82	82	10.9	235	151	23,600	338	3
80	86	86	12.6	180	155	27,400	342	1
								18
			Site index 60 feet at 50 years					
40	53	65	7.5	68	21	1,000	25	8
50	60	66	7.7	213	69	4,300	86	12
60	66	68	8.3	300	112	10,300	172	13
70	70	71	9.5	268	132	16,400	234	—
80	74	74	10.6	229	140	19,700	246	—
								33
			Site index 50 feet at 50 years					
50	50	58	7.4	68	20	1,000	20	4
60	55	59	7.6	174	55	3,200	53	3
70	59	60	8.0	240	84	6,600	94	—
								7

* Stump height, one foot; top diameter inside of bark, 6 inches. Bark is not included in volume.

For example, a comparison of 50-year stands having site indexes of 70 and 50 shows average heights of 68 feet and 47 feet; average diameters of 7.0 inches and 4.6 inches; average basal areas of 133 square feet and 98 square feet; average volumes of 4,060 cubic feet and 2,140 cubic feet; average annual growth of 81 cubic feet per acre and 43 cubic feet, but only 495 and 856 trees per acre.

Each site index class is divided into 10-year age classes from 20 to 80 years. The aspen forests, like plants and animals, increase in height, in diameter, in basal area, and in volume per unit area as they increase in age, and the increases are more rapid in the high site index classes than in the lower. The number of trees per acre, however, decreases rapidly as the stands grow older and the smaller, weaker trees are killed out in the struggle with their larger, stronger neighbors for light, water, and nutrients. On the average site, this reduces the number of trees per acre from 2,300 at 20 years to 295 at 70 years.

Composition of the Stand

In every forest and in any stand, there are trees of different sizes. In aspen forests, which are usually composed of trees of approximately the same age, the trees of average size are most numerous, and the number both larger and smaller than average becomes progressively smaller. In the 55-year age and 62-foot site index classes in well stocked stands, the average is 495 trees to the acre, distributed among the diameter classes as follows:

Diameter breast high in.	No. of trees per acre	Diameter breast high in.	No. of trees per acre
4	7	8	119
5	42	9	52
6	109	10	12
7	154	Total	495

The distribution of sizes varies at different ages and on different sites, but tends to follow the same general scheme. The largest number of trees are of average size and those larger and smaller than average decrease progressively.

The principal value in knowing the number of trees of different sizes is in the knowledge of the number of trees that, because they are above certain diameters, are usable for commercial purposes. For most uses at the present time aspen becomes merchantable when it is 6 or 7 inches in diameter. The numbers of trees per acre of these sizes and larger at each age and in each site index class are shown in the yield tables for board foot contents in trees 6 inches and over (Table II), and in trees 7 inches and over (Tables III).

The number of aspens per acre varies widely in stands of the same site and age. These variations are often referred to as differences in degree of stocking, or density. They may be due to one cause or a combination of causes—the origin of the stand, whether from seedlings or suckers; the number and intensity of fires that may have killed a part of the trees; or the use for grazing, which thins out the young trees.

This variation in number of trees per acre may be illustrated by figures from a large number of measured stands of different densities. The number of trees per acre 6 inches and more in diameter, in the plots less than 50 years old, commonly vary as much as 150, both above and below the average number in well stocked stands for any given age and site, as shown in Table II. Expressed in another way, the actual stands deviated 75 per cent above and below the average for well stocked stands. The stands more than 50 years old, almost without exception, had less than the average number of trees 6 inches and more as compared with well stocked stands. Several plots had 150 trees per acre less than the well stocked stands, and in some cases even 250 or 300 less. As an example, the average well stocked stand at 40 years with site index 60 (Table II) has 215 trees 6 inches and over in diameter to the acre; yet stands of this age and site were found to have from 350 to 50 trees. If all trees of one inch and over are included, the well stocked stands had 980 to the acre; the average on those not selected to represent good stocking was about 700.

The density, or degree of stocking, as judged by the number of trees to the acre, is also influenced by the proportion of other species—pine, balsam fir, or spruce—that may be mixed with the aspen. These usually occur as an understory of small trees. If they are numerous the stocking is more dense than if it were judged by the number of aspens alone. The stands that were more than 40 per cent overstocked were those in which the overstocking was due to an understory of conifers. This effect on the density of the mixture of smaller conifers was also illustrated by stands that were 75 per cent understocked with aspen but were overstocked when all species were included.

The number of trees per acre has been commonly used as the basis for classification. Hansen (1923) considered "normal" or well stocked stands of seedlings to have from 1,000 to 2,000 stems to the acre, from 800 to 1,500 saplings, and from 500 to 800 poles. On this basis he found the following percentages of aspen-paper birch stands in the normal, overstocked, and understocked groups for each of the three size or age classes:

Size class	Normal per cent	Overstocked per cent	Understocked per cent
Seedlings	28	15	57
Saplings	45	27	28
Poles	38	48	14

His standard for normal, or well stocked, stands is lower than that used in this study, as is indicated by a comparison of his figures—500 to 800 trees per acre in the pole stage representing an average age of 30 years with the density of 1,400 trees to the acre in well stocked stands on an average site at 30 years, in Table I. Allowing for the predominance of seedling stands that he found, and combining seedling, sapling, and pole stands for both aspen-birch and aspen-birch mixed with conifers, about 45 per cent of the area of aspen-birch type in St. Louis County, Minnesota, is occupied by understocked stands.

The Michigan Land Economic Survey assigned the forest areas to classes of good, medium, and poor stocking. The classes were not defined by number of trees per acre, but good stocking included stands that would yield good grades of merchantable timber. For the aspen-birch area in the counties of Antrim, Roscommon, Alpena, Ogemaw, and Menominee, in a part of the region where the aspen stands are generally spoken of as poor and scrubby, they found 76 per cent of good stocking, 17 per cent of medium stocking, and 7 per cent of poor stocking. Their sample acres in Ogemaw County show 560 trees at 10 years, 1,410 at 15 years, and 870 at 27 years. These densities would not justify their inclusion with the well stocked plots used for the yield tables.

The survey of the Wisconsin Land Economic Inventory in two townships of southern Bayfield County indicates about 35 per cent of the aspen-paper birch type fully stocked, 30 per cent medium, and 35 per cent sparsely stocked. That a large part of the aspen area is well stocked may be explained and confirmed by the fact that fires, which have been so prevalent and are so large a cause of the extensive areas of aspen in the region, do not decrease but rather increase the density of the new crop of aspen. On the whole, probably about a third of the total aspen area in the region has a sufficient number of trees to the acre to be considered well stocked for growth; not more than a fourth is so poorly stocked that it will not produce a merchantable stand at maturity.

GROWTH AND YIELD

Well Stocked Stands

Well stocked stands contain a sufficient number of trees well distributed over the area to form a nearly complete crown canopy (Fig. 4). These stands, because of a more or less uniform spacing of the trees and an equal start, produce at a given age and on a given site a large percentage of the total number of trees of about average diameter. Stands of this character produce high yields.

The development of well stocked aspen stands in respect to average height, diameter, basal area per acre, and yield per acre for the 40, 50, 60, 70, and 80 site index classes and for 10-year age classes, are shown in Tables I, II, and III. Table I gives figures for total yield in cubic feet of all trees one inch or more in diameter; Table II, the yield in board feet of trees 6 inches and more in diameter by the International Log rule; and Table III the yield of trees 7 inches and more in diameter, by the Scribner Decimal C rule. The tables also show the average annual growth per acre for each age and the average total height of the dominant trees, which is used in determining the site index. Table IV contains figures on the yield per acre in cords of 8-foot wood

Well stocked stands in which the trees average 6 to 8 inches in diameter will produce 50 cords per acre in 40 years where the site index is 80; 55 cords in 50 years where the site index is 70; 44 cords in

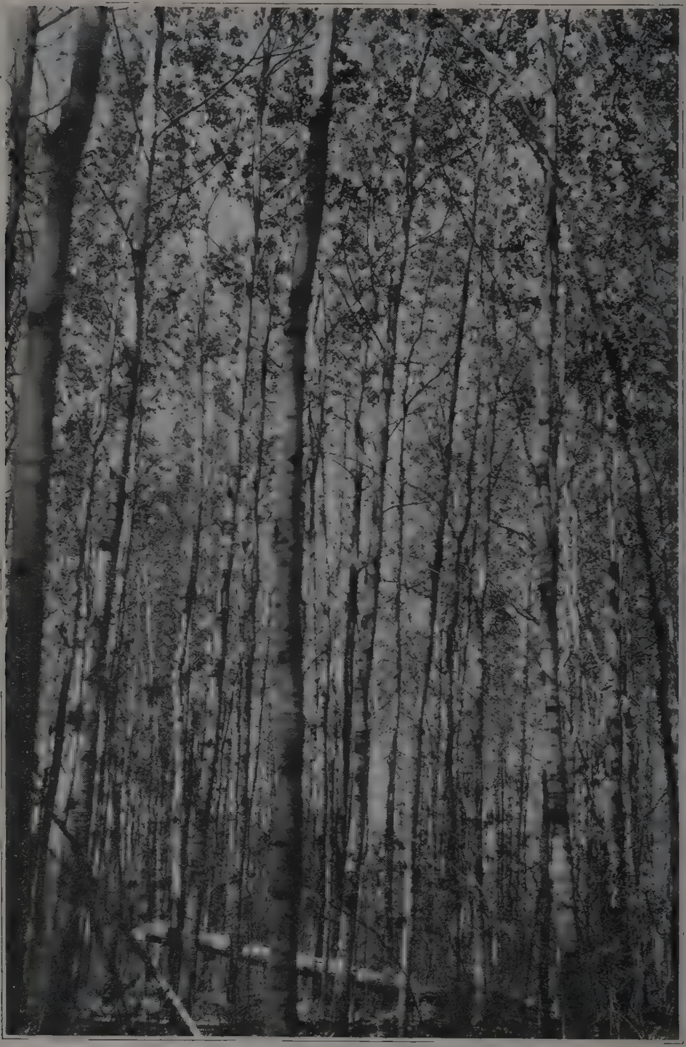

Fig. 4. Well Stocked Aspen 40 Years Old

Experimental cutting areas seeded to white pine and white spruce. Chippewa National Forest, Minnesota.

50 years where the site index is 60; and 33 cords in 60 years where the site index is 50. The mean annual growth at 50 years on the average site represented by site index 60 is 64 cubic feet, about 9/10 cord per acre. On the good sites the growth at the same age may be 94 cubic feet, or 1¼ cords, and on the poor sites even in well stocked stands the

growth is only from 22 to 43 cubic feet, or 1/10 to 1/2 cord per acre per year, respectively.

TABLE IV

Cordwood Yields for Well Stocked Aspen in Trees 4 Inches and More in Diameter at Breast Height

Age	Av. total height of dominant trees	Av. diameter at breast height	Basal area per acre	Peeled volume per acre*	Av. annual growth per acre
years	feet	inches	sq. ft.	cords†	cords†
Site index 80 feet at 50 years					
20	46	3.3	88	9	0.45
30	59	4.8	110	32	1.07
40	71	6.3	129	50	1.25
50	80	8.1	143	63	1.26
60	87	10.3	153	71	1.18
70	93	12.6	161	76	1.08
80	98	14.3	165	80	1.00
Site index 70 feet at 50 years					
20	40	2.9	83	5	0.25
30	51	4.2	102	25	0.83
40	62	5.4	120	43	1.07
50	70	7.0	133	55	1.10
60	76	9.0	144	63	1.05
70	82	10.9	151	67	0.96
80	86	12.6	155	69	0.86
Site index 60 feet at 50 years					
30	44	3.5	94	12	0.40
40	53	4.5	110	30	0.75
50	60	5.9	122	44	0.88
60	66	7.6	133	51	0.85
70	70	9.3	139	55	0.79
80	74	10.6	143	57	0.71
Site index 50 feet at 50 years					
40	44	3.5	88	11	0.27
50	50	4.6	98	26	0.52
60	55	5.8	105	33	0.55
70	59	7.1	109	37	0.53
Site index 40 feet at 50 years					
50	40	3.2	60	5	0.10

* Stump height, one foot; top diameter inside of bark, 3 inches.

† Standard cord 4x4x8 feet, close piling. Volumes in cords were obtained by applying the factors used for conversion of merchantable volumes in cubic feet to cords to corresponding average diameters at breast height. As a check, the same results were obtained from curved distributions of stems of different sizes per acre for a given age. The latter curves were also used for obtaining volumes in cords for stands with average diameter less than 4 inches.

Altho the data from which the growth figures were derived were taken largely in Minnesota and northwestern Wisconsin, they are probably applicable also to aspen stands throughout the northern part of Michigan and of Wisconsin. This is confirmed by the few stands measured in Marquette County, Michigan, by the data of the Land Economic Survey in Ogemaw County, Michigan, which indicate site index 56 and good stocking; and by figures for Antrim County, Michigan, by Buttrick (1923), which indicate mean annual growth at 30 and 38 years of 2/3 to 1 1/10 cords per acre per year. It is interesting to note for comparison that Schotte (1916) found stands of the closely related aspen in Sweden producing 1½ to 2 cords per acre per year. The latter figure exceeds the most rapid growth found in the Lake States, which was 1 7/10 cords per acre per year in a 50-year stand in Lake County, Minnesota.

Several important conclusions may be reached by a study of the yield table figures. If the trend of diameter growth in Table IV, site index 40, were extended, it would be found that the trees would not reach an average merchantable size for pulpwood (about 6 inches) until 80 years. The average annual growth on these poor sites is only 1/10 cord per acre. Moreover, the rot in aspen on an average site increases rapidly after 60 years and amounts to 20 per cent of the volume of the trees at 70 years, according to Schmitz and Jackson (1927). It seems probable that the decay will be as serious on poor sites as on average sites, if not more serious. Therefore it is inadvisable to plan to grow aspen on these sites until they are 70 or 80 years old, because they may not survive to those ages. On the other hand, if the aspen is cut at 50 years the trees will average less than 4 inches in diameter. It may be concluded, therefore, that the growing of aspen for pulpwood on lands of site index 40 and probably also on those of site indexes less than 50, will result in disappointment or failure.

For the possible production of aspen lumber, Table III, showing the board feet in trees 7 inches and more in diameter by the Scribner Decimal C rule, is a conservative guide. On site index 80, well stocked stands should produce 14,200 board feet at 50 years; on site index 70, 9,600 board feet at 50 years; and on site index 60, 10,300 board feet at 60 years. The yields for these comparatively small trees, by the Scribner Decimal C rule, are notably low for mills that saw carefully and utilize closely the small material. The following comparison of the yields in board feet at 50 years by the Scribner rule (Table III) with those by the International rule (Table II), which includes also the 6-inch trees, shows the conservatism of the Scribner figures.

Site index	Scribner	International
80	14,200	21,200
70	9,600	16,700
60	4,300	10,700

On site index 40, aspen will not produce enough trees more than 6 inches in diameter to provide an appreciable yield. On site index 50, at 70 years, it will produce only 6,600 board feet, by the Scribner rule. Even this amount would have to be discounted by at least 20 per cent for decay. As with cordwood, therefore, it is not likely to be profitable to grow aspen for lumber on site indexes less than 55.

Where paper birch predominates in mixture with aspen or occurs in almost pure stands, the growth and yield figures for aspen are not directly applicable. In order to indicate the development, growth, and yield of paper birch, areas were selected from the 38 that were measured to represent relatively pure and well stocked paper birch stands. The figures are given in Table V. The average dominant height on these areas corresponded to aspen site indexes between 50 and 60. In general, paper birch on corresponding soils has a lower site index value, grows more slowly, and yields less at the same age than aspen. This is indicated by the fact that paper birch plots, as a whole, may be represented by a site index of about 53—the average for the aspen plots was 64. In other words, the average dominant tree at 50 years in a paper birch stand would be 53 feet high; aspen on the same area would be 64 feet. If the yields at 55 years and site index 60 are compared, paper birch would produce 38 cords to the acre and aspen 47 cords in well stocked stands.

TABLE V

YIELD OF RELATIVELY PURE, WELL STOCKED PAPER BIRCH STANDS, WITH AVERAGE DOMINANT HEIGHT CORRESPONDING TO SITE INDEX CLASSES 50 AND 60 OF ASPEN

Age, years	Site index class			
	50		60	
	No. of trees 6 inches and more	Av. number of cords per acre	No. of trees 6 inches and more	Av. number of cords per acre
30	10–30	8		
40	50–100	15	150–250	25
50	150–250	21	300–400	35
60	200–350	26	300–400	40

Volume tables giving the contents of standing trees of paper birch in total cubic feet, merchantable cubic feet to a 3-inch top diameter, and cords were prepared from analyses of 116 paper birches and are included in Tables XVIII, XIX, and XX, in the appendix.

Understocked Stands

The density, or number of trees per acre, which has been discussed, is not the most reliable index of stocking for use in the prediction of growth or yield of aspen, because the relation between changes in number of trees per acre and increase in volume as the stands grow older is not consistent. Better measures of the degree of stocking are afforded by basal area, total volume, or average annual growth per acre. Basal area, or the sum of the areas of the cross-sections of the stems of the trees at breast height reduced to an acre basis, is the simplest measure to compute and to use. It was used as the criterion of stocking in the preparation of the yield tables and in comparisons of understocked and overstocked with well stocked stands. The relation between increase in basal area and in volume is sufficiently definite that changes in basal area may be used for rough predictions of changes in volume.[3]

In preparing yield tables, which include columns of basal area per acre, plots were eliminated that were less than 69 per cent[4] stocked as compared with the average for each 10-foot age and 10-foot site index class. The areas measured without regard to good stocking of aspen were more than 25 per cent understocked by basal area of aspen in 93 out of 144 cases, or 65 per cent. If conifers are included in the basal area, only about 8 per cent of the plots were understocked by as much as 25 per cent. It is estimated that in comparison with the averages for well stocked stands given in the yield tables, two-thirds of the area of the aspen-birch forest is understocked and grows less rapidly in volume than is indicated in the yield tables.

Understocking may cause a serious inaccuracy in the prediction of growth by the use of the yield tables. Altho only a few areas examined were less than 50 per cent stocked, the use of yield tables on these areas can not be recommended. A wide difference is obtained between the well stocked stands on which the yield table is based and the poorly stocked stands. For example, a 34-year-old stand was found on a site indicated by the average height of the dominant trees to have an index of 44, and the basal area, the number of trees, and the volume were all below that given by the yield table for this age and site index. The basal area was 35 square feet, only 56 per cent of the 63 square feet given in the yield table. There were only 170 aspens per acre that were one inch and more in diameter, as compared with the normal of 1,880, or only 9 per cent. In volume, the stand had 405 cubic feet, 42 per cent of the 960 cubic feet given by the yield table. Such a comparison clearly shows the danger of applying yield tables based on well stocked stands to poorly stocked stands.

A further indication that yield tables are unsuitable for stands like the example given is that open growing trees usually form large, bushy crowns at the expense of their growth in height, so their average dominant height is not a true index of the site. For instance, the site index of 44 for the stand described is low. The soil and vegetation showed that the true site index for this area would have been at least 58, if the stand had been fully stocked. The effect of understocking on the height growth and, therefore, the site index in badly understocked stands, may often be difficult to detect, hence the use of the yield tables as a basis for predicting growth by basal area in stands more than 50 per cent understocked is not recommended.

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[3] This method neglects relatively small differences in the stands caused by changes in form and height.

[4] The ± 31 per cent deviation from good stocking represented twice the standard deviation of the distribution of the plots about the mean.

Understocking may be evident, also, in its effect on the size of the average tree in the stand as well as on the number of trees, basal area, and volume per acre. Usually the average tree is larger in an understocked stand than in a well stocked stand of the same age and site index class. For example, one plot 66 per cent stocked by basal area and only 25 per cent by number of aspens one inch and more in diameter per acre, had an average diameter of 8.9 inches as compared with 6.4 inches for the well stocked stands of corresponding age and site. This relationship is sometimes reversed, but not often. The high yields of fully stocked stands are due in no small degree to the large number of trees per unit of area.

The use of yield tables for the prediction of growth involves (1) the determination of the age of the stand and of the site index from the relation between the average height of the dominant trees and the age. The site index should be checked by noting the other species of trees and the ground cover associated with the aspen and by the character of the soil. (2) An inventory should be made from representative strips or sample areas to show the number of trees per acre of different diameters. From this inventory the basal area per acre may be determined by the use of tables of basal area or areas of circles. (3) The computed basal area should then be compared with the basal area for the same age and site index class as shown in the yield table and the percentage calculated of the actual stand as compared with the well stocked stand. (4) The volume that a well stocked stand would have at 10, 20, 30, or more years in the future may be obtained from the tables. Multiplying this figure of future volume by the percentage of actual present stocking by basal area, an indication of the yield of the understocked stand for 10, 20, or 30 years in the future will be obtained. An example will make the calculation clearer. Plot 15 was found to be 27 years old and had a site index of 70. Its basal area from measurement of the diameters of the trees was 73.5 square feet. The well stocked basal area for site index 70 and 27 years (Table I) is 97 square feet. The stand is therefore 76 per cent stocked. It is desired to know what this stand may be expected to produce when it is 50 years old. The volume of a well stocked 50-year stand on site index 70 is 4,060 cubic feet. Multiplying 4,060 by 76 per cent gives 3,086 cubic feet, the predicted volume of the stand after 23 years, when it becomes 50 years old.

The calculated future yields of understocked stands obtained in this way are usually less than actual yields, because as the more open stands grow older, fewer trees are crowded out and the trees grow more rapidly in diameter than in fully stocked stands. This method of predicting yields is reliable and its conservatism may often be desirable to compensate for unforeseen damage or losses.

Overstocked Stands

Overstocking may be defined in several ways. The most definite, altho an arbitrary way, is by comparison with the basal areas of well stocked stands in the yield table (Table I). The degree of overstocking may then be measured by the percentage by which the basal area of a given stand exceeds that of the yield table for the corresponding age and site index. Stands having not more than 31 per cent greater basal area than the average of the well stocked stands were included in the preparation of the yield tables. Overstocked stands may therefore be considered to include only those that have more than 31 per cent excess of basal area. This is undoubtedly a higher limit for overstocking than was set by Hansen (1923); consequently many stands classified by him as overstocked would not be so classified according to this standard.

Another approach may be made by considering that overstocking, to have any significance, should be indicated by measurable stagnation of growth in diameter, volume per acre, or height. Depression of height growth would lower the site index. Only one stand was found in which the apparent stagnation, from observation in the field, was confirmed when the measurements were worked up. In this case the height of the dominant trees at 36 years indicated a site index of 50. On this basis the plot had 71 per cent excess basal area. The vegetation and soil, however, showed conclusively that the site index should have been at least 62—overstocking had reduced it by 12 units. Additional evidence of error in the site index was provided by the number of trees per acre, which, in a stand so heavily overstocked by basal area, would be expected to be decidedly higher than the yield table value. Actually it was lower. This indicated that the stand belonged to a higher site index class, because the number of trees per acre decreases as the site index increases. Furthermore, the average tree was one inch larger in diameter than the yield table value for that age and site index. This again suggested a higher site index, because the average tree in an overstocked stand would ordinarily be smaller than the yield table average. The reassignment of this stand to site index 62 reduced the degree of overstocking from 71 per cent to 29 per cent and made consistent the relationship to the well stocked stands in number of trees per acre and in size of average tree. This effect of overstocking in reducing the height growth and consequently the site index may cause serious discrepancies in all comparisons with the yield table and in predictions of growth. As it is not easy to detect, all available means should be used to check the determination of site index figures derived from the average dominant heights. Fortunately, overstocking to a degree that will cause a serious depression of the site index is probably uncommon and limited to small areas.

The measured plots included only three that had more than 31 per cent excess of basal area as compared with the yield table. Excluding the one just cited, the other two, altho they had 34 and 35 per cent excess of basal area, respectively, showed no evidence of stagnation.

The stands that had more than 25 per cent excess of basal area show that this degree of overstocking, or 40 per cent excess in number of trees per acre as compared with the yield table, does not cause stagnation but results in proportionately higher yields. For example, a stand 47 years old with site index 69 had a basal area per acre of 178 square feet, or 38 per cent above the 129 square feet of the yield table. The plot had 800 trees above one inch in diameter to the acre as compared with the well stocked average of 570, a 40 per cent excess. There were 532 trees 6 inches and more in diameter per acre as compared with 390 for the well stocked stand. The total volume was 5,082 cubic feet per acre, 35 per cent above the normal of 3,760. The size of the average tree, however, was only 6.2 inches—a little less than the normal of 6.4. Both the basal area and the number of trees per acre clearly suggest the possibility of stagnation due to overstocking; yet the total volume and the average annual growth per acre of 108 cubic feet are as much in excess of the yield table value as are the figures for basal area or number of trees. The conclusion seems justified that overstocking in aspen to an extent sufficient to cause stagnation of growth is extremely rare, and is usually not operative even in stands that appear to be too dense for their best development.

MATURITY, ROTATION, AND LONGEVITY

The maturity of a forest may be determined technically by finding the age at which the average annual growth culminates and overtakes the current annual growth. On the average site for aspen the average annual growth culminates at about 50 years, when it amounts to 64 cubic feet per acre. The current annual growth for 10-year periods reaches a peak of 77 cubic feet per acre between 40 and 50 years and declines until it is exceeded by the average annual growth at about 50 years. This is a desirable age at which to cut the stands, provided the trees have reached sizes suitable for commercial utilization.

Rotation is a term used to express the approximate age at which forest stands will be cut. With aspen, a rotation of 50 years for site index classes 60, 70, and 80 corresponds to the age of maturity or maximum average annual volume growth, and also provides a high yield of trees more than 6 inches in diameter suitable for pulpwood, box boards, or small saw timber. In site index class 50, the trees do not reach an average diameter of 6 inches until after they are 60 years old. The rotation, therefore, would usually be not less than 60 years. On the poorest sites, represented by index class 40, it is doubtful whether aspen stands will survive long enough to become marketable.

For merchantable saw timber, a rotation of 60 or 70 years will usually be necessary. The average annual growth does not culminate until the stands are 70 years old or older. The longer rotations for saw timber are advisable only in the site index classes of 80, 70, and the upper part of 60.

After 60 years the average annual growth declines, owing to the death of the crowded trees. The larger trees in the stands, however, continue to increase in diameter until they become 100 years old or even a little older. The oldest well stocked stand measured was 85 years old, on site index 72. It had an average diameter of 12½ inches, and a maximum diameter of 17 inches. A patch of aspen that had come up in an opening in the old-growth pine forest before it was cut was 95 years old, 100 feet high, with trees up to 18 inches in diameter. Occasional trees are found as large as 20 inches in diameter. However, stands of aspen more than 75 or 80 years old are rare and have little importance.

Influence of Decay in Forest Management of Aspen

The development of decay in aspen was studied by Schmitz and Jackson (1927). By applying their figures of the average percentage of intermediate and final decay on an average site (site index 60) at different ages to the average annual volume growth from the yield table, the following figures of reduced or net annual growth are obtained.

Age, years	Av. gross annual growth cu. ft.	Decay, per cent	Av. net annual growth cu. ft.
40	61	7.7	56
50	64	11.2	57
60	64	15.7	54
70	61	20.5	49

The percentage of decay up to 50 years is not large enough to change materially the culmination of the average annual growth, which comes at about 50 years for net as for gross growth. The increasing rate of decay after 50 years emphasizes the advantage of harvesting aspen by that age wherever the trees are large enough to make their exploitation economically practicable. Furthermore, it shows that rotations of 70 years or more, such as would be required to grow aspen to merchantable size on poor sites, are inadvisable. Occasional stands as old as 75 years, however, have less than the average percentage of decay and produce good yields of saw timber. A good example is the stand 75 years old with site index 78 that was cut on the Chippewa National Forest for box boards in 1924 and 1925. This stand had less than 5 per cent of serious decay.

The question whether decay is more serious on poor sites than on good sites has not been answered. There is a general impression among those familiar with the region that the aspen goes to pieces earlier from decay or some other cause on poor sites than on good sites. This impression is confirmed by the distribution of the measured plots in relation to age and site index. In spite of the fact that a special attempt was made to obtain data representative of all the age and site index classes, none of those with site index less than 50 were more than 45 years old, those of site index between 50 and 55 were less than 60 years old, and the few plots over 74 years old had site indexes over 65. Schmitz and Jackson (1927), however, suggest from data regarding the prevalence of decay in trees of different sizes that the quality of site makes little or no difference. This question can not be answered satisfactorily until more definite evidence is available.

Summarizing the subject of maturity and rotation, it may be said that aspen will produce good yields of pulpwood in 50 or 60 years on site indexes higher than 55, and that stands on site indexes above 60 may often be grown to 70 years for the production of saw timber. On the other hand, aspen on site indexes less than 50 will probably never produce a merchantable crop of timber before a large proportion of the trees becomes unmerchantable from decay or other causes. An intermediate group of stands on site indexes between 50 and 55 may be grown to produce pulpwood on a rotation of 60 years, but can not safely be held for longer rotations to produce saw timber.

REPRODUCTION OF ASPEN

Aspen reproduces so abundantly by suckers that its seeding habits are comparatively little known. The "cotton" is produced in great quantities in most years by the female trees. Locally, however, only one in 30 of the trees may bear seed. One tree 1½ inches in diameter and 11 feet high had 213 catkins with an average of 22 fruit capsules on each catkin. With several or many seeds from each catkin, the seed production from a mature stand would evidently be enormous. The seeds mature about May 15 and fall from then until early in June. For this brief period the air may be full of the cotton and the ground covered with a mat of it. The small size of the seed and its fitness for wide distribution by the wind is indicated by the fact that there are

2½ to 3 million of the seeds to a pound. A large proportion of the seeds, however, at least in some years, do not mature. The viability of fresh fertile seeds is high but lasts not more than two or three weeks after they are mature. Germination begins within 12 hours after the seeds fall and is complete within a week if conditions are favorable.

Seedlings

In spite of the enormous production of aspen seed, the number of seedlings in most years is small. Apparently, seedlings start abundantly only in the occasional year in which good rains occur and the ground is thoroly moist during the brief period while the seeds are falling and retain their vitality.

The distribution of seed in effective quantities for long distances is illustrated by a stand, apparently of seedling origin, in northern Michigan. Seven years after a heavy cutting in an old-growth forest of sugar maple, there are on the average 2,218 aspens to the acre, averaging 16 feet in height and far overtopping the still more abundant reproduction of maple. Careful examination of the remaining old-growth forests adjacent does not reveal any aspen and apparently the numerous aspen seedlings originated from seed trees at a considerable distance from the area.

In general, however, so many of the seedlings die, even when seeds have been abundant, that the reproduction of aspen from seed is comparatively unimportant, especially in the production of a complete stand in the first generation. The abundant production and wide distribution of the tiny seeds are extremely important, however, in accounting for the extensive range of aspen and the small number of poorly developed trees in many stands of other forest types. In the northern Lake States seeding has been much less important in the creation of the millions of acres of aspen forest than has regeneration by root suckers.

Suckers

The preponderance of aspen forest in even-aged well stocked stands on areas known to have been burned repeatedly, is strong evidence of the part played by fires and of subsequent suckering. The vigorous growth of young trees the first year after cutting or fire would hardly be possible for aspen seedlings and affords further evidence of the origin of the stands.

The roots form a network of horizontally spreading laterals that are always within 2 feet and frequently within a few inches of the surface (Baker, 1923). The suckers develop from parts of the roots within 6 inches of the surface, after cutting or fire that kills the trees. Several suckers may come from the same root. Figure 5 shows a root of aspen 24 years old from which two suckers started where the root passed over a rock ledge and was covered by only a layer of leaf litter. The stems of the two suckers were 15 years old, that is, they started when a previous 9-year-old stand was killed by fire. The small roots that come off the main root near the suckers are from 9 to 12 years old and illustrate the characteristic formation of new roots near the point where each sucker develops. The specimen shown in Figure 5 was obtained in northeastern Minnesota; the point where the suckers came up was 10 or 12 feet along the root from the parent tree.

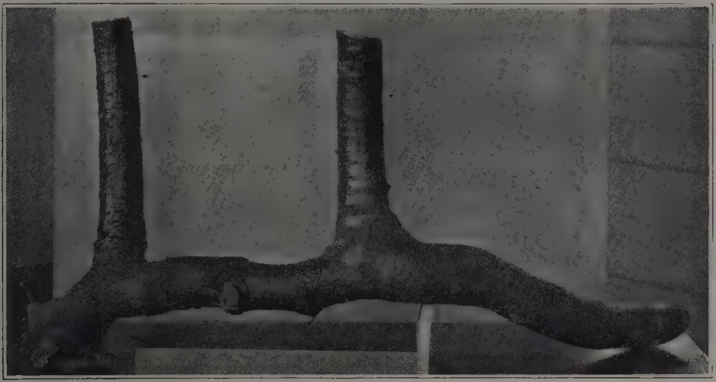

Fig. 5. Stems of Two Aspen Suckers, 15 Years Old, from Foot 23 Years Old, with Branch Roots 9 to 12 Years Old
Specimen loaned by courtesy of T. S. Hansen.

The number of suckers in the first one to 3 years after cutting or fire is large, and decreases rapidly as the trees grow older and the competition between them becomes more intense. Baker (1923) found more than 85,000 suckers to the acre at the end of the first year after spring cutting. The number decreased in the second and third years. The Dominion Forest Service, on experimental plots at Petawawa, Ontario, found that the number of suckers increased from the first to the third years after cutting and then decreased. On an experimental area in the Chippewa National Forest, cut clear in May, 19,060 suckers per acre were found at the end of the first year. Weigle and Frothingham (1911), working in Maine, found that after the ninth year dominant suckers in good condition were found only in stands of crown densities of 0.3 or less.

In the stands examined in Minnesota and Wisconsin that had produced any considerable number of suckers as a result of light fires or low density, the number of suckers increased with the age of the parent stand from 30 years to a maximum at 70 years, and then decreased as the vigor of the parent stand declined. The maximum number of suckers found per acre was 4,500 in a 70-year-old stand that had 170 aspens more than one inch in diameter to the acre. Even at 95 years, one stand had 2,300 suckers of recent origin to the acre.

The relation of the number of suckers to the density of the parent stand is less well marked than the relation to age. The number of suckers decreases and rarely exceeds 600 to the acre in stands that have more than 250 trees to the acre. Two exceptional cases were found, however, in one of which a stand of 420 trees had 1,200 suckers to the acre, and in the other, a stand with 700 trees to the acre, 50 years old, had 150 suckers. The number of suckers increases as the number of trees in the parent stand decreases below 250 to the acre. In stands of 150 trees, about 1,000 suckers to the acre were found on the average and in those of 100 trees, about 1,200 per acre. A 39-year-old stand on an experimental area in the Chippewa National Forest had, before cutting, from 137 to 1,020 suckers per acre. This indicates that in well stocked stands 40 to 65 years old with more than 250 trees to the acre there are from one to 3 suckers for each large tree. After cutting 292 out of 424 trees, or 69 per cent, 4 suckers for each cut tree came up the first year. After cutting 233, or about half the trees, 27 suckers per tree came up. After clear cutting of the 640 trees per acre, 30 suckers per tree developed the first year.

General conclusions as to relationships between suckering and age, density, season and degree of cutting, and fire in the parent stand can not be drawn from the limited data available, but the data are ample to show the tremendous capacity of the aspen stands to regenerate themselves by suckering after cutting or fire.

MANAGEMENT OF PURE ASPEN AS A PERMANENT CROP

A large part of the aspen in the northern Lake States consists of comparatively well stocked stands, most of them less than 20 years old, but with considerable areas up to 40 or 50 years old and already of merchantable size. Allowing for some poor stocking, these stands over considerable areas should produce from 10 to 30 cords to the acre at 40 to 50 years of age, or even more on the medium and good sites, represented by site index 55 or over.

In order to carry the younger unmerchantable stands to maturity, protection from fire is essential. Even a light fire kills many of the aspens and indirectly causes the early death of most of those that may survive for a few years. If the object of management is to obtain a new crop of aspen after cutting, it is only necessary to cut all the merchantable material; the new crop of suckers will provide ample and prompt regeneration.

The cost of growing aspen is low. It establishes itself without cost. Land values on the rocky or stony soils and on the better soils in the northern parts of the region that are not yet needed for agricultural development, are or should be not more than $1.00 or $2.00 an acre. If taxes are assumed to be 10 cents per acre per year, fire protection 3 cents, and the yield 20 cords to the acre in 40 years, the crop of aspen will earn 6 per cent if it has a stumpage value when cut of $1.93 per cord. It will earn 5 per cent if it has a value of $1.39. If on a poorer site, where it requires 50 years to produce 20 cords to the acre, it will earn 5 per cent if the stumpage value is $2.41. Prices of standing aspen, sold in 1926 in Minnesota for cordwood, ranged from 25 cents to $1.00 per cord, with an average of 75 cents; and for lumber, from $1.00 to $3.00 per 1,000 board feet, with an average of $2.25 (Wackerman, 1926). It is not unreasonable to anticipate that aspen 20 or 30 years in the future will have values of $1.50 to $2.50 per cord. Tables VI and VII show the future stumpage values that aspen must have to earn 3, 4, 5, or 6 per cent interest under different combinations of taxes, yields, and rotations. For any company or owner who has a use or a market for aspen, its management as a crop for pulpwood is not unattractive.

TABLE VI

ASPEN STUMPAGE VALUES PER CORD AT 40 YEARS

Yield per acre, cords	Annual taxes plus 3 cents fire protection, per acre					
	8 cents	13 cents	18 cents	23 cents	33 cents	43 cents
		To earn 3 per cent				
5	$2.11	$2.86	$3.62	$4.37	$5.88	$7.37
10	1.06	1.43	1.81	2.19	2.94	3.69
20	0.53	0.72	0.91	1.09	1.47	1.84
30	0.35	0.48	0.60	0.73	0.98	1.23
		To earn 4 per cent				
5	3.04	3.99	4.95	5.89	7.79	9.68
10	1.52	2.00	2.47	2.94	3.89	4.84
20	0.76	1.00	1.24	1.47	1.95	2.42
30	0.51	0.67	0.82	0.98	1.30	1.61
		To earn 5 per cent				
5	4.35	5.55	6.75	7.98	10.38	12.80
10	2.17	2.78	3.37	3.99	5.19	6.40
20	1.09	1.39	1.69	1.99	2.59	3.20
30	0.72	0.93	1.12	1.33	1.73	2.13
		To earn 6 per cent				
5	6.18	7.74	9.28	10.83	13.93	17.03
10	3.09	3.87	4.64	5.41	6.97	8.52
20	1.54	1.93	2.32	2.70	3.48	4.26
30	1.03	1.29	1.55	1.80	2.32	2.84

TABLE VII
Aspen Stumpage Values per Cord at 50 Years

Yield per acre, cords	Annual taxes plus 3 cents. fire protection, per acre					
	8 cents	13 cents	18 cents	23 cents	33 cents	43 cents
			To earn 3 per cent			
10...........	$1.58	$2.14	$2.70	$3.27	$4.39	$5.52
20...........	0.79	1.07	1.35	1.63	2.19	2.76
30...........	0.53	0.71	0.90	1.09	1.46	1.84
40...........	0.39	0.54	0.68	0.82	1.10	1.38
			To earn 4 per cent			
10...........	2.44	3.21	3.97	4.75	6.26	7.79
20...........	1.22	1.60	1.99	2.37	3.13	3.89
30...........	0.81	1.07	1.32	1.58	2.09	2.60
40...........	0.61	0.80	0.99	1.18	1.57	1.95
			To earn 5 per cent			
10...........	3.77	4.82	5.86	6.91	9.00	11.10
20...........	1.89	2.41	2.93	3.45	4.50	5.55
30...........	1.26	1.61	1.96	2.30	3.00	3.70
40...........	0.94	1.20	1.46	1.73	2.25	2.75
			To earn 6 per cent			
10...........	5.80	7.26	8.71	10.16	13.08	15.97
20...........	2.90	3.63	4.35	5.08	6.54	7.98
30...........	1.93	2.42	2.90	3.39	4.36	5.32
40...........	1.45	1.81	2.18	2.54	3.27	3.99

NATURAL CONVERSION OF ASPEN TO CONIFERS

Considering the large areas on which aspen is now unmarketable and the probable oversupply for some years to come, the conversion of aspen to less abundant and more valuable species requires thoro consideration. The proportion of the aspen-birch lands that have appreciable numbers of white or Norway pine, white or black spruce, balsam fir, or northern white cedar with or under the aspen, in the northern Lake States region, is estimated at between 10 and 20 per cent. Certain areas that have had special protection from fire, such as the National Forests in Minnesota (Fig. 6), the State Forest in Vilas County, Wisconsin (Fig. 7), and an area near Drummond, Wisconsin, where cut-over pine lands have been protected from fire by the company owning them, have considerable numbers of conifers on 30 or 40 per cent of the aspen type. More commonly, however, wide areas of the aspen type have only a negligible number of conifers in mixture.

Of the conifers that make up the 15 per cent of the aspen type being converted naturally, balsam fir is the most aggressive. Considering as a whole the area where aspen was mixed with conifers in St. Louis County, Minnesota, Hansen (1923) found the percentage of representation of the different species to be, for balsam fir 54, for Norway pine 20, for spruce 14, and for white pine 12. These proportions vary in different parts of the region and depend to a considerable extent on the composition of the old growth that was cut. The mixtures

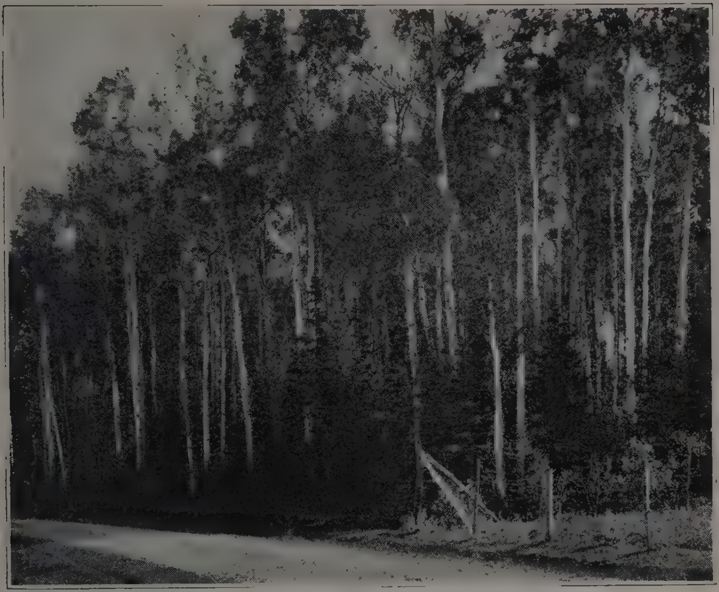

Fig. 6. Natural Conversion of Aspen-Birch to Balsam Fir
St. Louis County, Minnesota

of Norway pine and aspen are usually found on sandy, gravelly soils where the old stand contained considerable proportions of Norway pine. Black spruce occurs with the aspen in the margins of black spruce swamps, particularly in northeastern Minnesota. White pine is the

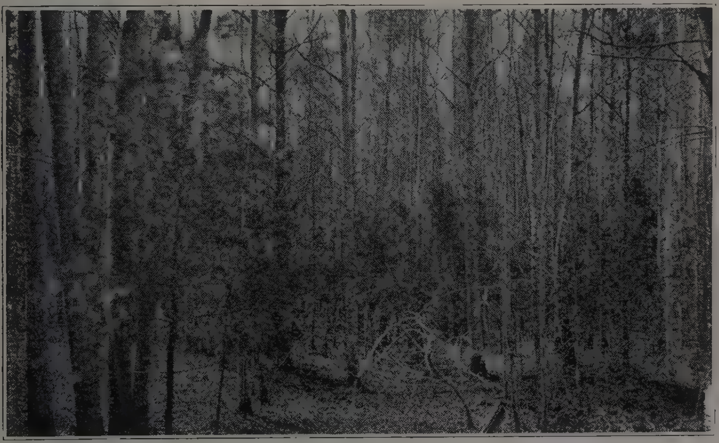

Fig. 7. Natural Conversion of Aspen to Norway and White Pine
Oneida County, Wisconsin

predominating associate of aspen in the belt through north central Wisconsin and Minnesota where heavy white pine stands were logged. Similarly, white spruce with the aspen is found most commonly in northern Minnesota in areas where white spruce predominated in the original forest (Kenety, 1917).

On the whole, if only 15 per cent of the area of the aspen type is being converted naturally to conifers and of that 15 per cent, balsam fir, the least valuable, contributes the largest part, natural conversion does not offer a prompt solution of the problem of the aspen lands. Is the proportion of the aspen type that contains a mixture of conifers increasing? If so, how fast, and what are the prospects that it will increase more rapidly in the future? Several elements affect the process and will be considered separately.

Advance Growth in Original Coniferous Stands

Large areas of the stands of old-growth white and Norway pine and white spruce and balsam fir were sufficiently open or irregular that seedlings of those species had become established in considerable numbers before the timber was cut. There were usually enough to form a new stand. Seedlings of balsam fir, white spruce, and white pine, most of which were established before the cutting, were found by Robbins (1928) at the rate of 456 to 3,074 to the acre on an area cut over 3 to 5 years previously at the eastern end of the Upper Peninsula of Michigan. Counts of 1,300 to 21,500 white pine seedlings to the acre under stands of old-growth white pine have been cited. An examination of the cut-over areas on the Chippewa National Forest, shortly after the cutting, showed the existence of a large amount of advance growth (Zon, 1912). It is almost always evident in the remaining stands of old-growth pine and spruce that have not been recently burned. The age of many of the larger conifers associated with the aspen indicated that they were survivors of the advance growth, which started before the original stand was cut and escaped subsequent fires. Except for the fires, most of the aspen-paper birch area would be covered with second-growth pine, spruce, and balsam fir from the advance growth in the old stands.

Source and Supply of Coniferous Seed

The old stands of pine or spruce bore seed abundantly, at least every few years. After the seed years, a good supply of seed was on the ground at the time of logging, especially on areas of white pine, because part of the seed does not germinate until the second season. The early logging left almost all the balsam fir and the pines and spruces that were too small to be merchantable but still large enough to bear seed.

These trees scattered seed after logging, altho that source of seed has gradually diminished as the trees have been wind-thrown or destroyed by fire. They also provided some shade on the cut-over areas. On the whole, therefore, the few years immediately after logging and before the aspen cover was complete were favorable for the seeding and establishment of the conifers. The age of the conifers in the present aspen stands shows that a considerable part of the pine and spruce was established at the time of or just after the old cutting.

Seed Trees

Some medium-sized and most of the defective trees of all sizes of pine and spruce were left at the time of logging and survived many years. They have served as seed trees, altho they were not left for that purpose. They have scattered considerable quantities of seed periodically in seed years. Altho most of the seed is eaten by rodents or birds, an occasional seedling starts under the aspen and promotes the process of natural conversion.

White and Norway pine and the spruces do not begin to bear seed in any quantity until they are 5 or 6 inches in diameter and 30 or 40 years old. The trees must be considerably larger before they are thoroly effective as seed trees. A moderately large seed tree of white pine produces from 12,000 to 25,000 seeds every 3 or 4 years (Fig. 8). A Norway pine seed tree produces 25,000 to 50,000 seeds every 6 or 7 years. The winged seeds are disseminated in considerable numbers for 300 to 500 feet from the parent tree. Notwithstanding these considerable quantities of seed, the remaining seed trees are not wholly effective, for there are rarely as many as 1,000 coniferous seedlings to the acre in the aspen stands near seed trees that have been producing seed for many years.

Few seed trees are left on the aspen lands and they are usually isoalted or in widely scattered groups. Considerable numbers of white and Norway pine remain on the Chippewa National Forest, where they were reserved, and on other state and national forests where they have been protected. Elsewhere, the small number of seed trees is one of the principal reasons for the unsatisfactory progress of natural conversion.

The relation between the number of established coniferous seedlings in aspen stands and the number or distance or direction of the parent seed trees is not definite. It has doubtless been obscured by the occurrence of fires and other causes of loss. On one area that had 10 white pine seed trees within 300 feet and at an average distance of 130 feet from the plot, only 200 seedlings to the acre were found. Good reproduction of white pine from seed trees was found on plots

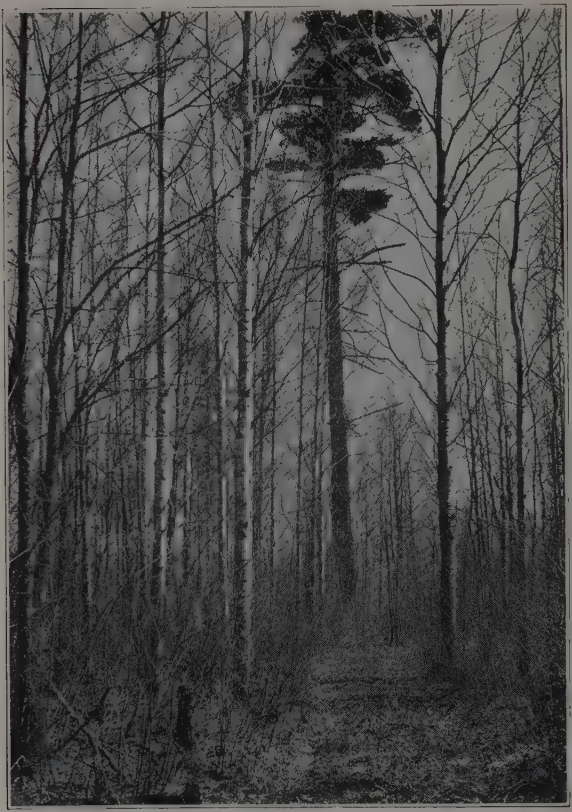

Fig. 8. Aspen Stand with Large White Pine Seed Tree
Chippewa National Forest, Minnesota

in Cheboygan County, Michigan, only where there were more than 5 seed trees to the acre; the Norway pine reproduction was poor, even with as many as 14 seed trees to the acre (Cashen, 1923). A careful count of the seedlings on permanent sample plots in a 40-year stand of aspen on the Chippewa National Forest showed that 3 good white pine seed trees on 2 acres had produced only 200 seedlings to the acre in 9 years and were therefore only partially effective in reseeding. On another plot with 53 seed trees within 200 feet, or 10 to the acre, 748 seedlings had started in the 9 years. On a third plot, 8 seed trees to the acre, chiefly to the northwest and southwest, whence the prevailing winds blow, produced 1,300 seedlings to the acre. The conclusion is suggested that at least 4 good seed trees to the acre, the equivalent of a spacing of about 104 feet, and probably 7 to 10 to the acre, spaced about

70 feet apart, are needed to provide adequate natural reproduction in the aspen type.

Except in occasional small areas, the seed trees remaining on the aspen lands are too few and too widely scattered to convert the millions of acres to coniferous species in any reasonable period of time. The poor character of many of the trees left after logging, resulting in small production of seed; the large number that have died since logging; and the periodic occurrence of seed years, which only occasionally synchronize with favorable moisture and other conditions, make the establishment of coniferous reproduction from seed trees slow, irregular, and generally unsatisfactory. These are not the only elements, however, that influence the process.

Effect of Rodents and Other Forms of Animal Life on Establishment of Conifers

The interacting influences of the many forms of animal life in the forest on the processes of forest regeneration and development are extremely complex. Certain obvious things about them are known, such as the damage caused during the periods when certain forms of animal life become overabundant in relation to their food supply. In some ways animal life in the forest may be beneficial. Birds and squirrels and probably other animals carry and distribute tree seed. Some seeds that they hide and fail to find germinate and thus help in the dissemination of those species. Unquestionably, the lower forms of animal life, like the insects, protozoa, and bacteria, are sometimes extremely important in controlling outbreaks of higher forms that are doing great damage to the forest, and in maintaining and promoting desirable physical and chemical qualities in the forest floor and soil.

For the most part, however, available information about the effect of animal life in the conversion of aspen bears upon its influence in hampering the establishment of the conifers. The lack of abundant or even satisfactory reproduction of pine and spruce in the aspen stands is certainly due in part to the scarcity of seed left to germinate. Red squirrels, ground squirrels, chipmunks, mice, and certain finches, such as the grosbeak and the crossbill, regularly eat conifer seeds, particularly those of the pines. Instances are cited by Pulling (1924) of poor and even of good seed years in which red squirrels cut all the cones on white pine seed trees days or weeks before maturity. The large proportion of Norway and white pine cones collected on the ground from caches or immediately after they are cut by squirrels offers additional evidence. In aspen stands where few seed trees are left, the rodents and birds undoubtedly get most of the seed in poor seed years and a large part of it even in heavy seed years.

Additional concrete evidence is provided by the seed spots of white pine and white spruce under 40-year aspen on the Chippewa National Forest. Part of the spots were protected by wire screens of one-quarter inch mesh for comparison with those not protected. The germination percentage for white pine at the end of the second season was increased as a result of screening from 2½ per cent to 8 per cent where the forest floor was left, and from 5 per cent to 22 per cent where it was removed. For white spruce the increase was from 9½ per cent to 15 per cent. There was evidence that some small rodent had burrowed under the buried edges of the wire and come up under the screens, so the protection was probably not complete. Even so, the considerable increase in seedlings may be attributed to the protection of the seed from rodents. At the Petawawa Experiment Station, in Ontario, similar protection of seed spots with wire screens gave an enormous "catch" of coniferous seedlings.

Hardly less important than the effect on seed supply is the direct damage done by various animals to established coniferous seedlings. Deer, when they become abundant, may browse the foliage of coniferous trees, as they have done in the aspen type in Itasca State Park, Minnesota. Squirrels and birds occasionally nip off the terminal buds (Hosley, 1928). Porcupines gnaw the bark from the upper parts of the trees and sometimes girdle them, so the tops are killed. These are minor forms of damage, however, and have not been serious in the northern Lake States. Grazing sheep, goats, cattle, or horses, especially if they are confined in a limited area, are almost certain to damage and kill a part or all of the coniferous growth within their reach. This damage is localized near farms and will be serious only locally as long as a large part of the aspen type remains unsettled.

The most serious animal damage that has occurred recently was caused by snowshoe rabbits when they increased to enormous numbers in 1925 and 1926 and at intervals of 6 or 7 years prior to that time. The damage by the rabbits is done chiefly in late winter or spring when the snow crusts over and they are forced to feed on the tops of the coniferous trees between 1 and 4 feet high that project above the snow. The best evidence of damage by rabbits may be found in plantations of pines made at various places in northern Minnesota in the aspen-birch type. Near Orr, in Itasca Park, and on the state and national forests in northeastern Minnesota, hundreds of acres of plantations were so nearly destroyed that only an occasional stub of a planted tree with its foliage partly or completely eaten off could be found (Fig. 9). Unquestionably, the natural reproduction of pine and spruce in these localities suffered as much. The damage to white spruce, white and Norway pine, black spruce, and balsam fir at Cloquet, Minnesota, has

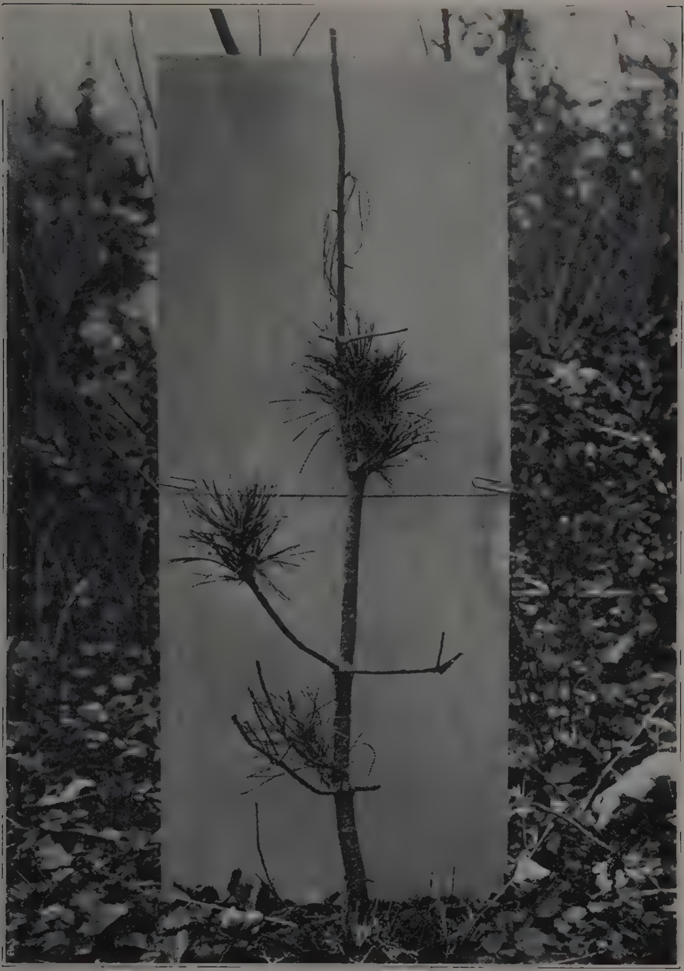

Fig. 9. White Pine Damaged by Snow-Shoe Rabbits

been reported by Corson and Cheyney (1928). Their conclusions coincide with those from a more extensive study by the Lake States Forest Experiment Station, in which all the species, with the possible exception of balsam fir, which is distinctly less susceptible than the others, were found subject to serious damage by rabbits. The rabbit damage in Wisconsin and Michigan was less severe, altho it was noted in 20 out of 30 of the white pine plantations in the aspen type. Sometimes 90 per cent of the trees were injured, altho more commonly less than half were damaged. Many of the damaged trees would, apparently, recover.

The rabbit damage was heavier near swamps and in brushy thickets where the rabbits, concealed from their enemies, abound. The 6- or 7-year intervals between the years of abundance, when the rabbits do the greatest damage, unfortunately are not long enough for the conifers under the aspen to grow above their reach. If these peaks in the rabbit population continue to occur at 7-year intervals, they offer a serious obstacle to the conversion of aspen to conifers.

Effect of Fire in Preventing Establishment of Conifers

Forest fires are chiefly responsible for the scarcity of conifers and for their absence over large areas of the aspen lands. One slash fire like those that covered the pine areas just after cutting destroyed most of the advance growth under the old forest. Repeated fires since have destroyed the few trees that escaped the first fires or that have subsequently germinated. Fires have also destroyed the seed trees that were left, and it is only because of their thick, resistant bark that the larger white and Norway pine seed trees have survived. Howe (1912) gives striking examples of similar conditions in Nova Scotia, where fires destroyed the coniferous growth and prevented or retarded its re-establishment on burned areas occupied by aspen and paper birch. As repeated fires increase the density of the aspen cover by replacing the older stand with a denser young stand, they probably in this way still further hamper the introduction of conifers. Effective fire protection is a first essential for the conversion of the aspen type.

The Aspen Forest Floor

The accumulation of leaf litter and humus in aspen stands unquestionably affects the establishment of the conifers in several, and probably conflicting, ways. The forest floor varies from a negligible thickness just after a fire when the new crop of aspen suckers starts, to 3 or 4 inches in dense stands of 50 years. It is usually about one inch thick. Several determinations on samples of one square foot from stands 20 to 55 years old have shown that the oven-dry weight of the forest floor amounts to from 4 to 30 tons to the acre. Obviously this layer of organic matter, which is highly absorptive of moisture and comparatively rich in plant nutrients, must have important influences directly and indirectly on the establishment of the conifers.

One immediate effect of the forest floor is detrimental. The germination percentage after the second season, in seed spots of white pine and white spruce, was increased by the removal of the forest floor in the following average percentages on 4 plots: (1) 2.5 to 5, (2) 8 to 22, (3) 1 to 9.5, and (4) 0 to 15. Seed sown in a potted soil sample of the forest floor from the same area gave only 3 per cent germination of white pine and 10 per cent of Norway pine from seed that gave 14 and 66 per cent, respectively, in adjacent pots of soil from pine stands. Experimental plots in Ontario, where seed was sown on burned soil, on hacked soil, and on undisturbed soil, indicate rather conclusively the advantage of hacking the soil. Poor results were obtained on the undisturbed forest floor and by complete destruction of the forest floor. Hacking was more favorable than burning. The unfavorable effect of the forest floor may be due to several causes, of which two well established ones may be mentioned: (1) The excessive drying of the forest floor during periods of drouth when its moisture content may readily be reduced to a point at which newly germinated seedlings whose roots have not penetrated the mineral soil would succumb. (2) Aspen leaves, after they fall and are compacted by the snow during the winter, form a mat that may easily smother small seedlings.

Effect of Shading and Competition with Other Vegetation

Many coniferous seedlings under stands of aspen die, from the time of their establishment for several years. This may be due to several causes, which are not distinguishable but would certainly include shading and root competition of the aspen and other tree species and of the shrubs and herbaceous vegetation. Fungi and micro-organisms take their toll. Excessively high temperatures in open stands and periods of extreme drouth also cause losses. The combined effect of these causes often results in the death of more than half the coniferous seedlings that germinate in any year. Definite evidence on this point is available from the three annual counts of reproduction quadrats in the 40-year aspen stand with white pine seed trees on the Chippewa National Forest. Many new seedlings were found and marked in 1925. One year later the losses had been 27 per cent in the plot with one third of the overhead cover removed, 66 per cent in the plot with one half the cover removed, 38 per cent in the uncut plot, and 17 per cent in the clean cut plot. The percentages dying of the total number of seedlings established from 1918 to 1924 on the corresponding plots amounted to 17, 26, 25, and 25, respectively. These heavy losses are not more than balanced by new germination after good seed years.

If the records of the 40 white pine underplantings from 5 to 15 years old in aspen stands are classified according to the amount of tree cover, the average losses were 50 per cent in stands with 5 to 24 per cent cover, 37 per cent in those with 25 to 60 per cent cover, and 54 per cent in those with 65 to 80 per cent cover. These figures suggest (1) that the lack of shade in the open stands of aspen results in losses from heat or frost; and (2) that too dense cover causes equally heavy losses, owing either to lack of light or to root competition of the overhead stand for moisture.

The possible damage to pine seedlings by excessive heat at the surface of the soil in the open has been demonstrated. The experiments of Toumey and Neethling (1924) showed that surface soil temperatures of 122 degrees to 139 degrees F. or more were often fatal to young seedlings of white and Norway pine. They obtained many readings above 122 degrees and a maximum of 152 degrees in southern New Hampshire. Gleason (1917) recorded the following temperatures in an aspen area in Cheboygan County, Michigan, during the hot weather in July, 1917, when the air temperature went above 100 degrees F.

Location of thermometer	In open, degrees F.	In aspen thicket, degrees F.
Bare surface soil	140	...
Ground debris	125	107
Shade of brake fern and herbs	112	109
Two inches in the soil	101	85
Four feet high, shaded	...	106½
Four feet high, in sun	...	108

Evidently the heat at the surface of the soil in openings in the aspen forest may injure or kill small pine seedlings when the maximum air temperatures in the shade exceed 90° F. Conversely, some aspen cover favors the pines by preventing such losses.

Further evidence of the effect of aspen cover is found in the aspen stands with a natural understory of conifers. All the aspen stands that had more than 200 conifers to the acre of any species were understocked on the average from 30 to 40 per cent by basal area. The detrimental effect of aspen-birch cover on the establishment of conifers is noted by Howe (1912) in Nova Scotia. On an area run over by a ground fire after being cut 10 years previously, where 2 white pine, 6 red spruce, and 2 balsam fir seed trees remained to the acre, a square rod yielded 27 fir seedlings, 19 white pine, and 5 red spruce. Adjacent birch-poplar (aspen) thickets averaged only 2 white pine seedlings to the square rod. On the other hand, in comparison with other types of cover, the Michigan Land Economic Survey, in Ogemaw County, concluded that aspen favors pine reproduction. They report, "Almost all of the white and Norway pine seedlings found in the county were under stands of poplar" (aspen).

Experiments by the Dominion Forest Service in Ontario with natural seeding of white pine in stands of birch and aspen have led to the preliminary conclusion that there is no difficulty in obtaining reproduction but that seedlings do not survive more than one or two years. Experimental cuttings have shown that open stands after cutting have better coniferous reproduction than those left uncut. Direct seeding also gave best results under the more open stands. In those having 30 to 40 square feet basal area reserved, only 9 to 15 per cent of the seedlings died; in those with 50 to 60 square feet basal area, 19 to 26 per cent died.

The relation of the amount of coniferous reproduction to the density of the brush is not well defined, altho the tendency is for the number of seedlings to decrease as the brush density increases. Most of the areas with an appreciable number of small conifers had brush densities of not more than 0.3. This general statement applies to white pine, Norway pine, balsam fir, white spruce, and black spruce. The notable exception was one plot having 1,350 white pines to the acre with a brush density of 0.6. The smaller number of conifers in brushy areas may be due, not directly to the brush but to the greater damage by rabbits, which abound in such areas. On the other hand, the root systems of hazel and large-leafed aster in Itasca Park occupy almost completely the upper 6 inches of soil, from which Lee (1924) concludes "that the failure of reproduction of the pines is largely due to the presence of this thicket undergrowth. This fact is well indicated by the presence of many one year old pine seedlings and the entire absence of seedlings of any greater age. During the spring, which is usually rather dry, the soil moisture in the surface layer would easily be exhausted by this heavy-foilaged undergrowth. Then the dense shade, combined with a critical desiccation would be sufficient to kill the feeble pine seedlings."

The general conclusion may be drawn that except for the first few years after fire or cutting, the conifers do not increase in number as the aspen stands grow older. The number may, however, remain nearly constant or fluctuate from year to year as the older seedlings that die are replaced by new ones.

Growth of Conifers in Aspen Stands

The characteristic feature of pine, spruce, and other conifers associated with aspen is their small size in comparison with the aspen. All the conifers grow more slowly in height, diameter, and volume, at least during the first 20 years, than does aspen. This is true even when the conifers are growing in the open and are not suppressed by a larger stand of aspen. Jack pine is the one exception. It grows nearly as rapidly as aspen from the beginning and unless it keeps pace with the aspen in height growth it soon succumbs. Consequently, where jack pine is found in mixture with aspen it is usually in group-wise mixtures in which the jack pine is as large as the aspen. This mixture occurs commonly only in northeastern Minnesota and will not be considered further because jack pine is not likely to be useful in the conversion of aspen to conifers.

The other conifers—white and Norway pine, white and black spruce, balsam fir, and northern white cedar—are sufficiently important to require detailed consideration of their growth in height, diameter, and volume in comparison with that of aspen.

Height Growth

The heights attained by the different conifers at successive ages are shown in Table VIII for the two classes of trees that, for lack of specific terms, have been called "crowded" and "not crowded." The "crowded" trees include those that grew in comparatively dense stands or in groups of larger aspen and consequently were retarded in growth by shade and by root competition. The "not crowded" trees are those that grew in understocked aspen stands or in small openings of denser stands. They had some light from above and suffered less from root competition. The first significant point indicated by the figures is that all conifers grow slowly in height during the first 20 years. This is partly an inherent characteristic, particularly in balsam fir and the spruces, and partly the result of suppression by the aspen, which overtops them. As a result, at 15 years of age, when the aspen averages 22 feet high, the white and Norway pines are only from 3 to 10 feet high, the spruces and balsam fir from 2 to 6 feet, and northern white cedar one foot.

TABLE VIII

Height Growth of Aspen and Associated Conifers

Age	Aspen		White pine		White spruce		Norway pine		Balsam fir	
	Site index		Not crowded	Crowded	Not crowded	Crowded	Not crowded	Crowded	Not crowded	Crowded
	50	60								
years	Average total height, feet									
10	14	15	4	2	3	2	5	3	4	1
20	26	29	13	6	11	5	17	9	11	4
30	36	40	28	15	25	12	31	20	25	10
40	44	49	39	25	37	22	41	28	43	22
50	52	58	46	32	46	30	49	34	54	33
60	58	65	51	36	52	35	54	38	60	42
Basis, number of trees	..	..	103		33		37		158	

The average number of years required for the four principal conifers to attain a height of 4½ feet in "crowded" and "not crowded" conditions was as follows:

Species	Not crowded, years	Crowded, years
White pine	10	18
Norway pine	11	15
Balsam fir	16	24
White spruce	16	22

This information is often useful in connection with determinations of total age of larger trees. The appropriate figure from the table is added to the number of rings at breast height to obtain the total age.

From 20 years of age to 50 or 60 years, the pines, white spruce, and especially balsam fir increase more rapidly in height but, owing to their slow start, the two most desirable species, white pine and white spruce, remain 15 to 25 feet shorter than the aspen up to 50 or 60 years. Only an occasional pine or spruce is as tall as the aspen at these ages, usually because they had passed their early period of slow growth in the original stand before the aspen started.

These comparisons apply to white pine, white spruce, and balsam fir, which occupy approximately the same average site as aspen. Norway pine, however, attains the heights shown in Table VIII on poorer sites represented by site index 55 for aspen. Norway pines that are not crowded, therefore, may be expected more nearly to overtake the aspen on these sites at 50 years. The other conifers may also maintain their growth as the growth of the aspen declines on the poorer sites, altho available data do not afford proof of the possibility. The suggestion is probably justified, however, that conversion of aspen to conifers is more likely to have a successful outcome on the poorer sites for aspen.

After the aspens are 60 or 70 years old they begin to die out, openings in the stand are formed, and the conifers take advantage of the increased space and continue their height growth until they are more than 100 years old.

The height growth of the crowded conifers is strongly influenced by the amount of space they have. At 60 years they average about 17 feet shorter than trees that have not been crowded. Badly suppressed trees may be considerably shorter at the same ages than are the average "crowded" trees. In extreme cases, white pine or white spruce trees were only 10 to 12 feet high at 40 years. The crowded trees, in general, can not be expected to overtake the aspen.

At early ages the pines are taller than spruce or balsam fir, which are noted for their slow growth in height at the beginning. Later, white spruce and especially balsam fir rapidly improve their original stunted height growth to such an extent that the fir is the tallest of the 4 species from 40 or 50 to 60 years.

The growth in height of white pine, measured on 27 plantations 5 to 15 years old, may illustrate the effect of the density of the aspen cover on the height growth of that species. Where the aspen-birch cover occupied less than 40 per cent of the area, the average annual height growth was 0.34 foot; under 60 to 80 per cent cover it was 0.21 foot. The average annual height growth of planted white pines under or close to the crowns of larger aspens or birches was 0.28 foot, as compared with 0.36 foot for those not directly suppressed.

The most significant fact in the comparative height growth of conifers and aspen is that the conifers, with the exception of the "not crowded" trees on the poorer sites, remain below the aspen and do not overtake it until the aspen stand begins to deteriorate.

Diameter Growth

The growth of conifers is more variable in diameter than in height because it is more affected by the density of the stand and the degree of suppression. Table IX gives the average diameters of the four important kinds of conifers at different ages for "crowded" and for "not crowded" trees. Northern white cedar grows more slowly than these four. Up to 30 years, Norway pine shows the most rapid diameter growth because it is found in aspen stands only where it has had an opportunity to grow in openings. From 40 to 50 years, as the openings close and the competition between the larger trees becomes more intense, its rate of growth becomes less than that of the other conifers, showing its greater susceptibility to crowding. White pine and white spruce increase in diameter for the first 40 years at about the same rate. Thereafter the white pines average larger, probably because only those survive that have relatively ample growing space, while more of the spruces live and grow slowly as suppressed trees. Both species have an average diameter of 6 or 7 inches in 60 years—some trees 11 or 12 inches. An average diameter of 7 inches in a stand of pine or spruce represents a merchantable stand wherever there are enough trees to the acre to provide a merchantable volume for cutting. The diameter growth, therefore, indicates that a merchantable understory of white pine or white spruce may be produced in aspen stands that are not too dense in 60 or 70 years. As the aspen begins to die at 70 or 80 years, giving the conifers more space and light, there is good reason to believe that the pine and spruce would maintain and possibly increase their diameter growth for another 20 or 30 years.

TABLE IX
DIAMETER GROWTH OF CONIFERS ASSOCIATED WITH ASPEN

Age	White pine		White spruce		Balsam fir		Norway pine	
	Not crowded	Crowded	Not crowded	Crowded	Not crowded	Crowded	Not crowded	Crowded
years	Average diameter breast high, inches							
20	1	..	..	..	1	..	2	1
30	4	2	4	2	3	1	5	3
40	7	4	7	3	6	3	7	5
50	9	5	8	4	8	4	9	6
60	11	6	10	5	10	6	..	..
Basis, number of trees	124		40		158		40	

Volume Growth

The growth in volume of trees, as a composite of growth in height, diameter, and form, is for that reason more variable than the growth in either height or diameter and consequently average figures are less satisfactory. They have little significance except in connection with the number of trees per acre, which is also extremely variable. The volume, or yield per acre, which is the product of these two variables, gives the most useful practical information. The average volume per acre of conifers of all species increased with age from 230 cubic feet, or about 3 cords to the acre, at 30 years to 420 cubic feet, or 5 cords, at 50 years and 550 cubic feet, or 6 cords, at 60 years. Individual areas showed wide variations due to causes such as the origin and fire history of the stands, which had affected the number of trees to the acre.

Volume production is not determined primarily by the density of the aspen, except that the volume of the conifers is uniformly low in stands of aspen that are denser than the average for well stocked stands. No essential difference is found, however, between the stands from 0 to 30 per cent understocked and those that are more than 30 per cent understocked. Several stands that were from 0 to 30 per cent understocked had comparatively large volumes of conifers. For example, in one 60-year stand of aspen there were 1,100 cubic feet, or about 12 cords, of conifers to the acre, and in two 75-year stands there were, respectively, 1,220 cubic feet, or 14 cords, and 1,817 cubic feet, or 20 cords. The largest volume of balsam fir recorded on any one area was 18 cords in a 65-year old stand of aspen that was 33 per cent understocked. The best white spruce volume was 11 cords to the acre in a 60-year stand of well stocked aspen. Of white pine, 2,500 board feet to the acre was found in a 47-year stand of aspen 45 per cent understocked; and of Norway pine, 980 board feet in a 41-year stand of aspen 9 per cent understocked.

The figures for volume per acre, like those for diameter, indicate that it is possible to produce merchantable stands of spruce and pine in 60 to 75 years if they are started and grown under a cover of aspen, in addition to the yield of aspen from the same area.

As the stands grow older the aspen gradually disappears, and after 70 years its place is taken by the conifers. Thus the stands change in character, cease to be recognizable as aspen, and would be classified as pine or spruce. In this period the conifers increase rapidly in volume, particularly in merchantable board-foot volume.

The transition from aspen to white spruce is illustrated in Table X from data by Kenety (1917), who considered that the plots represent the white spruce type.

The rate of growth in diameter of white spruce in aspen stands (Table IX) indicates that at least the "not crowded" trees would attain diameters of 11 or 12 inches in 100 years. Kenety's data show that only 38 trees to the acre of this average size yielded 12 cords, with 13 cords additional of aspen that was still living.

TABLE X

ACRE PLOTS OF ASPEN-WHITE SPRUCE*

Age, yrs.	Trees per acre more than 4 in. in diam. breast high	Av. diam. breast high in.	Av. height, ft.	White spruce Yield		Balsam fir Yield		Aspen Yield		Total Yield	
				Cords	1,000 board feet	Cords	1,000 board feet	Cords	1,000 board feet	Cords	1,000 board feet
100	38	12.3	80	12	6	1	..	13	4	26	10
100	8	12.4	75	2½	..	12	1	13	4	27½	5
103	7	11.0	70	1	1	..	..	10	4	11	5
106	28†	15.7	87	15	7	14	..	8	4	37	11

* Data from Kenety, 1917.

† More than 9 inches.

Five cords to the acre in places where the timber is reasonably accessible is usually considered a merchantable stand of spruce. If this figure is assumed as the criterion of a merchantable stand, it is possible by the use of volume tables (Cloquet, 1926) to indicate roughly how many trees of different average diameter to the acre would be required to yield 5 cords. The figures are given below in tabular form.

White Spruce

Av. diameter breast high, in.	Volume per tree, cords	Trees per acre to make 5 cords
6	0.04	125
7	0.06	83
8	0.08	63
9	0.11	45
10	0.15	33
11	0.20	25
12	0.24	21

These numbers, ranging from 125 trees 6 inches in diameter to 21 trees 12 inches in diameter to the acre and sometimes more, are found on small areas in natural stands.

With white pine it may be assumed that 5,000 board feet, mill tally, to the acre represents a merchantable stand. The number of trees of different average diameters required to yield 5,000 board feet to the acre is shown in the following tabulation.

The number of trees in this case, from 312 to 58, is larger than for white spruce but still well within those sometimes found in natural stands of aspen. An understory of numerous spruce or pine seedlings may easily pass unnoticed in a stand of aspen, whereas, by the time the conifers reach 50 years, the same number of trees would evidently form a good stand. In this way the future value of what appears to be a sparse reproduction of small conifers is often underestimated or entirely disregarded.

White Pine

Diameter breast high in.	Height ft.	Volume per tree (mill tally) bd. ft.	No. of trees to make 5,000 bd. ft. per acre
6	34	16	312
7	37	25	200
8	39	35	143
9	41	45	111
10	43	58	86
11	44	71	70
12	45	86	58

On the basis of diameter growth, number of trees, and volume per acre, it appears possible to grow a merchantable crop of white pine or white spruce in the aspen type, in from 60 to 100 years, either from natural reproduction or by planting a moderate number of trees to the acre.

Relation of Growth of Conifers to That of Aspen

The conifers under aspen are usually crowded. Their slow growth during the first 20 years, while the aspen is shooting up rapidly, is evident from a comparison of the figures given for the growth in height of conifers and of aspen. Altho conifers that are not too much crowded grow comparatively well even under the aspen cover, they continue to lag behind the aspen not only in height but also in diameter and hence in volume for the 50 to 70 years while the aspen is growing vigorously. Comparing them at 50 years on an average site, the aspen reached 58 feet in height while the white pine and white spruce reached an average of 40 feet. The difference in diameter and volume per tree is less marked. In volume per acre, however, owing to the smaller number of pine and spruce and to their small dimensions, the aspen had 3,220 cubic feet at 50 years, while white pine averaged only 310 and the other conifers only 420 cubic feet. Only after the aspen deteriorates from decay and old age, usually after 70 years, do the conifers overtake the aspen in dimensions and volume per acre. The figures in Table X for white spruce stands 100 years old are examples of the stage in the natural conversion of the aspen to white spruce at which the aspen has partly died out and the white spruce has just become the dominant tree.

The process of natural conversion is complicated by the different densities of aspen and by the several species and sites, all of which have their influence. As a result there is wide variation in the development of individual trees of pine, spruce, and balsam fir in the different areas studied and there is an even wider variation between the averages of the plots. These variations render generalizations unsatisfactory and unreliable. The one thing that stands out plainly is the slow growth of the conifers as compared with that of the aspen. Next is an evident tendency for conifers that grow in openings to develop more rapidly than those close to or under larger aspens. This is the reason that figures on growth of conifers were presented under two broad headings—"crowded" and "not crowded" trees. The same tendency was also indicated by the data from planted white pines discussed under "Height growth." From this evidence, the conclusion follows logically that the less dense, understocked aspen stands with openings between the trees are favorable for the growth of conifers. Furthermore, the conifers on sites poor for aspen are in a better position to maintain themselves and take the lead at an earlier age.

Development of Conifers and Final Outcome

If growth of the conifers started before that of the aspen, or if a supply of coniferous seed from adjacent stands or from seed trees was available, the conifers developed in sufficient numbers to form a merchantable stand in addition to the aspen in 60 or 70 years. The early stages in the process of seeding of white pine are illustrated by the figures from a permanent sample plot in a 40-year well stocked stand of aspen on the Chippewa National Forest, where there were 7 good white pine seed trees within 200 feet of the plot. All the white pine reproduction started after a light ground fire in 1918. Up to and including 1924, more than 80 white pine seedlings to the acre had become established. In 1925, 20 of these died and 160 new seedlings started, making 220 to the acre; in 1926, 80 died and 60 new ones started, making 200 to the acre; and in 1927, 20 died and no new seedlings were found, making 180 to the acre. Thus the balance fluctuates from year to year, with a gradual increase in the number of seedlings over several years. Fewer of the seedlings die as they grow older, so gradually the larger, more vigorous seedlings form an understory.

When the pine or spruce starts at the same time, the aspen takes the lead and forms an overwood for 60 to 80 years—sometimes longer if it is left uncut. On the poorer sites, where Norway pine and black spruce are more often associated with the aspen, it rarely maintains its lead for more than 50 or 60 years. On the better sites, where white pine and white spruce are the usual associates, the aspen may live and retain its lead for 75 to 90 years. The conifers, however, are all comparatively long-lived. Balsam fir regularly lives to 100 or 120 years, the spruces to 150, Norway pine to 200, and white pine to 250. They increase in diameter and volume up to 120 or 150 years. This ability of the conifers to outlive the aspens, together with their capacity to seed and grow under the aspen are the two characteristics that enable the conifers to start and grow, at first inconspicuously, and then gradually to occupy the space left as the aspens die and finally to replace the aspen so that the stand ceases to retain its character as aspen type and becomes predominantly pine or spruce and balsam.

The process of natural conversion of aspen to conifers, however slow, is nevertheless effective and will come to fruition without human intervention. Unfortunately, however, natural conversion is taking place in only 10 to 20 per cent of the area of aspen lands. Cutting and fires have done their work too well by destroying coniferous reproduction and seed trees on the other 80 to 90 per cent of the area. In most parts of the region there is not likely to be much increase in the area that will be converted naturally within any reasonable time. In what other ways may the process be extended and accelerated?

MAN'S ASSISTANCE IN THE CONVERSION PROCESS

The conversion of the aspen type requires human assistance to be promptly and widely effective (Fig. 10). There are several ways in which it may be applied—protection from fire, cuttings of various kinds, preparation of the ground for natural or artificial seeding, and planting.

Fire Protection

Protection from fire is a first essential for conversion. If the conifers are already established, a fire through the area will kill most or all of them and postpone the conversion for many years, until a new crop can start. Protection from fire, by preventing the destruction of the conifers and thus allowing them to mature, replace the aspen, and seed in additional areas, promotes the conversion process. If fires had been prevented in the past, there would be only a fraction of the present area of aspen, and that fraction would have a good representation of conifers in mixture. Effective fire protection in the future is essential for the natural or artificial extension of the conversion process.

Cuttings in Mature Aspen

Any cutting has several immediate effects in the aspen forest that directly or indirectly influence the conversion process. Cutting a part or all of the aspen creates openings in the canopy and allows more light to reach the smaller conifers and the ground beneath. The sun's heat causes higher temperatures at the surface and below the surface of the soil. As a result there is a more rapid decomposition of the forest floor. At the same time, the increased heat and easier circulation of air cause a higher rate of evaporation and drying out of the forest floor in periods of drouth. These results of cutting are not clearly distinguishable one from another, either directly or in their effect on the conifers. The intensity of the changes, however, depends on the degree of cutting, so they are greatest in clear cuttings and progressively less with lighter partial cuttings. Cutting of the aspen results within the next year in a regeneration of aspen suckers which, as has been shown, are extremely dense after a clear cutting and progressively less dense after partial cuttings until they are unimportant if less than a third of the aspen is removed. The change from the mature stand to the young growth of suckers mixed with brush and luxuriant herbaceous vegetation apparently results in less serious competition for the conifers, at least for a few years after the cutting.

Effect on Associated Conifers

The combined net effect of the changes brought about by cutting the aspen is favorable to the development of both seedlings and large trees of white pine, white spruce, and other conifers. Evidence in support of this statement is available from permanent sample plot records both on the Chippewa National Forest and at the Petawawa Forest Experiment Station, in Ontario. In Minnesota the 40-year well stocked aspen plots were cut over in May, 1926, with the results on the natural white pine reproduction indicated in Table XI.

TABLE XI
MORTALITY OF WHITE PINE SEEDLINGS

Degree of cutting	1926* seedlings in 1927†	1918-26* seedlings in 1927†	1918-26* seedlings in 1926† and 1927†
	per cent	per cent	per cent
Clean cut	0	5	5
50 per cent cut‡	11	5	42
30 per cent cut‡	29	9	24
Uncut	33	10	36

* Years of origin.
† Years of death.
‡ Percentages based on crown cover.

The Canadian experiments indicate conclusively that cutting favors coniferous reproduction. In one series, in which 50 to 60 square feet of basal area of aspen and birch were left, between 19 and 26 per cent died. On plots having 30 to 40 square feet of basal area reserved only 9 to 15 per cent died. Plots in another series (Veness, 1923) in 40-year aspen-birch type, cut in 1920 to leave 1,715, 1,278, and 600 trees to the acre, were undersown with white pine and white spruce and the 1925 counts showed that 68, 95, and 38 per cent of the seedlings, respectively, had died. The growth of the conifers under the reserved stands was notably slow.[5]

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[5] This information and that cited elsewhere from Canadian experiments without specific reference was furnished by letter through the courtesy of the Forest Service, Department of the Interior, Canada.

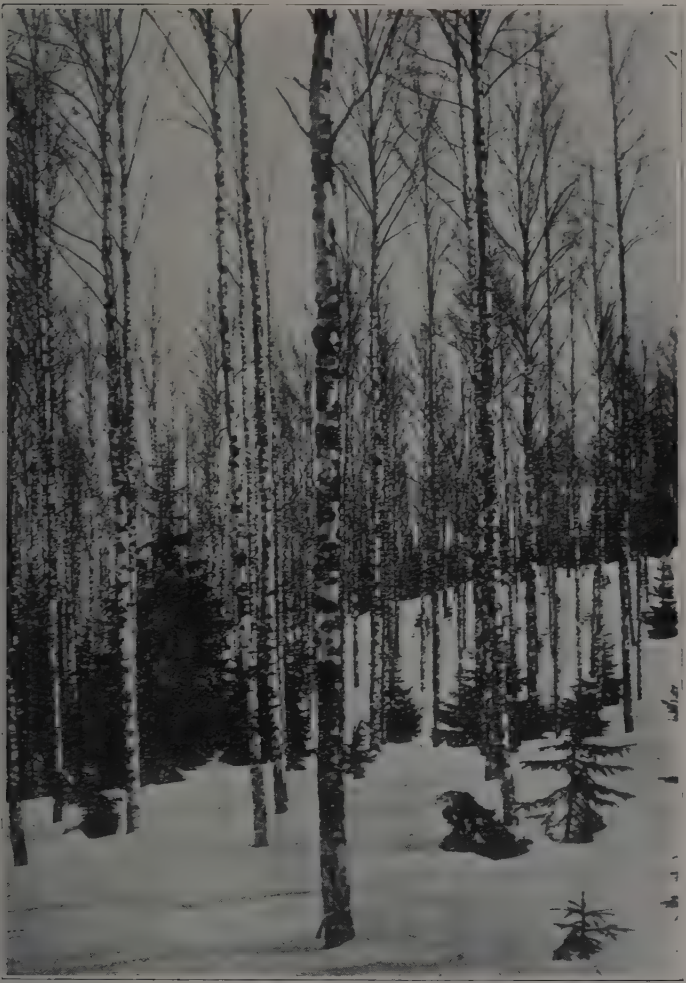

Fig. 10. Natural Conversion of Birch to Spruce Under Forest Management in Finland (Photo by courtesy of A. K. Cajander.)

In general, the heavier the cutting in the aspen the greater is the benefit in the survival and growth of white pine and other conifers. Clear cutting might on some areas and in some years result in damage to small seedlings by excessive heating of the surface soil or by sunscald. This statement is not substantiated by specific evidence, however, and such damage is probably prevented by the immediate regrowth of aspen suckers and other vegetation, which provide shade for the small seedlings. The larger conifers are least likely to be seriously damaged by the exposure. Ample evidence of the response of advance growth and larger conifers to release by the cutting of aspen and birch is available for white pine and spruce under somewhat similar conditions in the northeast, but not for the Lake States. It is reasonable to expect, however, that cutting of aspen in the Lake States would result similarly in stimulated growth of the conifers that had been suppressed

Losses resulting from logging aspen.—The conifers below merchantable size will almost inevitably suffer losses and damage when the larger aspens are cut. Swamping and skidding are likely to cover 10 to 25 per cent of the area and additional losses occur in connection with the felling. The heavier the cutting, the greater is the loss and damage. Clean cutting of a dense 40-year aspen stand in May resulted in the loss of 52 per cent of the white pine seedlings less than one foot high. Cuttings of 50 per cent or less in the same stand caused losses of less than 25 per cent of the white pine seedlings. On the whole, from 10 to 50 per cent of the conifers may be destroyed in logging. The damage and loss of the larger conifers that can easily be seen could be reduced, probably to less than 15 per cent, by care in felling and swamping, and in locating skidding trails.

The season in which the logging is done affects the conversion in two ways: (1) Winter logging on the snow eliminates most of the damage to and loss of seedlings less than one foot high that are covered by the snow. It may also increase the damage to small growth that projects above the snow and is easily broken in cold weather. (2) The season of logging affects the conifers indirectly by its influence on the number of aspen suckers that come up after cutting and compete with the conifers. Spring cutting produces the most suckers, summer cutting fewer, and fall cutting the fewest, according to Baker (1923). This effect of season soon disappears, however, because the number of suckers and their competition become equalized within 10 years after the cutting.

Release Cuttings

Any cutting made in the aspen before it is mature to release the smaller conifers in the understory from suppression by the aspen are included under this heading. Release cuttings presumably will increase both the survival and the growth of the conifers and thus enable them to reach merchantable size in a shorter time. As experience in the Lake States is again lacking, it is necessary to turn to the suggestive experience in the northeast, where white pine has been released from the competition of gray birch and red maple. Release cuttings may be carried out in several ways. One is to cut the aspens while they are still small and repeat the operation as often as may be necessary to save the pines and maintain their growth. By this method, the first release would be made when the aspen is only 3 or 4 years old. The cutting can be done cheaply with a machete, with which the stems are not completely severed. They are then bent over so that the roots are less likely to send up new sprouts. This operation should be carried out, preferably, in a season when the leaves are off, so that the smaller conifers may not be overlooked. The aspens should be cut that are close to the conifers and are already crowding or are likely soon to suppress them. Frequently the conifers occur in groups, and the release of a group as a unit is desirable. Altho no immediate return is obtained from such cuttings, they can be made more cheaply while the aspens are small than at a later time. On the other hand, a second release cutting may often be necessary within 10 or 15 years after the first (Cline and Lockard, 1925).

The second possibility is to postpone the release cutting to the latest time when a sufficient proportion of the white pine or other conifers may be expected to recover and benefit from the release—in New England, when white pine is 12 to 15 feet high and 10 to 25 years old, according to Spaeth (1922). It might sometimes be possible to obtain a money return from the small cordwood produced in the cutting, but this is unlikely at the present time in the Lake States. The chief advantage consists in avoiding a second release cutting after some years, which becomes unnecessary because the conifers are sufficiently tall that they will not be overtaken by the new crop of aspen suckers. Judging from the comparative height growth of aspen and the different species of conifers in the Lake States, the age at which to cut the aspen to accomplish this object would be between 15 and 25 years, or when the conifers are from 3 to 15 feet high.

Release cuttings may require from 1 hour to 2 days time for a man to the acre, depending on the number and size of the trees to be cut. The costs are ordinarily from $2.00 to $5.00 an acre (Fisher, 1918). Weeding of inferior hardwood for the benefit of pine gives the most productive results for the money expended of any intensive forestry work that may be carried on in New England, according to Hawkins (1924). He says that $2.00 to $7.00 an acre has been invested over large areas by a box company; in special cases $15 an acre has been spent to good advantage. Where conifers are established or planted, release cuttings must be considered as an aid or sometimes even a necessity in converting an aspen stand to conifers.

Disturbing the Forest Floor

That the aspen forest floor reduces the amount of germination of white pine, white spruce, and probably also of other conifers, whether naturally or artificially sown, has been indicated. Conversely, the removal of the floor in seed spots and the hacking or stirring up of the leaf litter by dragging brush increase the amount of germination. Hacking the forest floor gave higher germination than burning, in experiments by the Canadian Forest Service. Ordinarily, even if burning were effective in increasing germination, it would be inadvisable for several reasons.

The actual removal of the forest floor over considerable areas is not necessary and is undesirable because it would be costly and would deprive the soil of a valuable moisture regulator and fertilizer. The object is rather to stir up the forest floor in enough places that sufficient seeds to form a stand may find favorable germinating beds. Logging accomplishes this on a certain proportion of any area logged. In aspen stands that were to be sown before logging, dragging the tops of trees back and forth across an area, either as they were felled or with the smaller twigs trimmed off, would probably promote germination. Similar treatment in the autumn of a seed year should favor the natural reproduction of conifers. The benefit of such measures in relation to their cost has not been determined. Their possible value should, however, be considered in connection with any plan for conversion by natural seeding or broadcast sowing.

Sowing Seed

Direct sowing of the seed of conifers on the planting site has usually failed in the aspen type as elsewhere in the Lake States. Broadcast sowing has hardly a record of success, altho the preparation of the ground by hacking or dragging brush might be an aid in occasional favorable years.

Seed spot sowing has in some instances given satisfactory results. In an analysis of direct seeding methods for converting aspen and paper birch land to spruce and pine, Robertson (1926) gives averages for 17 experimental plots in Ontario. After 4 years, there were 340 seedlings per acre under dense shade, and 5,000 per acre under light shade. From intensive investigations in New Brunswick he concludes that the seed spot is the most economical and reliable of the direct seeding methods. It is not satisfactory, however, with white pine, because the comparatively large seeds are usually eaten by rodents. White spruce, on the other hand, was successfully spotted on recent burns under moderate shade and on north slopes. The seed-spot method may be recommended for use in the aspen-birch type on rocky shallow-soiled areas where planting would be difficult and costly. The costs in Canadian seed-spot sowing have usually been between $4.00 and $5.00 an acre. A slight additional cost would be necessary to thin out spots that had more than one tree at the time of the first release cutting. Experimental sowings of Norway and white pine in cleared spots one foot square, were not successful at Cloquet, Minnesota, on areas of young aspen mixed in the thick brush, where the hardwood leaves smothered the young seedlings (Kenety, 1917).

Seed-spot sowing of 10 seeds each of white pine and white spruce under 40-year aspen after different degrees of cutting on the Chippewa National Forest gave results in the second spring after the seed was sown as shown in Table XII. The experiment indicates that the removal or disturbance of the forest floor is essential for the germination of white spruce and only a little less necessary for white pine. Protection from rodents increases the success with both species. Protection by screening is impractical in an extensive reforestation operation; but without protection, the results, irrespective of the degree of cutting, are too poor for the method to be recommended.

TABLE XII
PERCENTAGE OF SEED SPOTS WITH ONE OR MORE LIVING SEEDLINGS

Kind of spot	Degree of cutting			
	Uncut	30 per cent cut	50 per cent cut	Clean cut
White Pine				
Natural forest floor	0	22	0	0
Natural forest floor screened	37	42	62	0
Forest floor removed	0	40	25	33
Forest floor removed and screened	75	83	75	50
White Spruce				
Natural forest floor	0	22	0	0
Natural forest floor screened	0	0	0	0
Forest floor removed	0	37	25	17
Forest floor removed and screened	25	100	100	50

Summing up available evidence on direct seeding, the method may have a use on rocky sites where planting is difficult and expensive. On such sites, seed-spot sowing of white spruce where there is a moderate amount of shade is suggested. Even under these circumstances the sowing should be on an experimental scale before a large operation is undertaken.

Planting in the Aspen Type

Some planting has been done under aspen in the Lake States. Records are available of 70 plantations from 5 to 10 years old of which 40 are white pine, 19 Norway pine, 6 Norway spruce, 3 jack pine, and 2 Scotch pine. The examples of jack pine and Scotch pine are insufficient as a basis for conclusions and neither species is recommended for planting on aspen sites. Norway spruce is believed to be less well adapted for planting in the aspen type in the northern Lake States than the native white spruce. Unfortunately, experience with white spruce plantings is limited; the older plantings were largely destroyed by rabbits in 1924 and 1925. Norway pine is not suited for underplanting and should be planted only on open or recently burned areas where the aspen is not too large and too dense. Its chief value is on the sandy, gravelly, dry sites where it grew originally and where the aspen stands are likely to be irregular and broken. The discussion of planting will be limited to white pine and white spruce, the two most suitable species for planting in the aspen type.

Favorable and Unfavorable Conditions for Planting

The shade of aspen and birch is favorable for white pine plantations when the density of the crown cover is between 0.3 and 0.7, and less favorable when it is below 0.3 or above 0.7. This applies to both survival and early height growth. The benefit of the moderate degree of cover in comparison with open sites is probably connected with the damage from excessive heat and frost that white pine seedlings suffer during the first year or two on exposed sites. The poorer results under aspen stands of more than 0.7 density are probably due to the competition of the larger aspen for light or root development. Hansen (1927) notes that the surviving planted white pines on a site with small aspen and thick brush were all in the open places or, conversely, chiefly those in the thickets died. This is further indicated by a comparison with planted pines immediately under or close to larger aspens that grew, on the average, 0.28 foot in height annually, while those in the openings grew 0.36 foot annually. A specific comparison may be made of two white pine plantations on the Alpena State Forest, in Michigan, similar in all respects except that one was planted under a 30-year stand of aspen with a density of 0.8 and the other where the aspen was only 5 to 10 feet high with a density of 0.5. In the first only 28 per cent survived and the trees averaged 0.6 foot high 4 years after planting. In the other, 64 per cent survived and the trees averaged 1.1 feet high. For natural reproduction, the more open stands of aspen and the areas immediately after cutting or fire offer more favorable sites for planting than the older, denser stands of aspen.

The slight effects of differences in soil on the survival of the planted pines are obscured by other factors. Growth tends to be less on the heavier loamy soils or on the low sandy soils near the water table, owing, probably, not so much to inherent qualities of the soil, as to the more serious damage by rabbits and the competition with other vegetation.

Snow-shoe rabbits are particularly abundant in the areas of young aspen stands and every seventh year, when they are particularly plentiful, they may almost completely destroy forest plantations, as they did in Minnesota in 1924 and 1925. The damage is more severe near the margins of swamps and less on dry sandy uplands (Corson and Cheyney, 1928). Rabbits are worse where the brush is thick than where it has been suppressed by a dense forest cover. If snow-shoe rabbits continue to be as abundant periodically as they have been in the past, control measures will be essential for the success of plantations in brushy areas in northern Minnesota and adjacent Wisconsin. The United States Biological Survey (Cox, 1911) suggested a method of poisoning to control the rabbits, but when the cost of control is added to the cost of planting and maintenance it may well be questioned whether planting is advisable on large areas of the aspen type.

Poor planting stock and careless planting may be causes of loss in any planting operation. They are, however, avoidable. The planting stock obtainable from the state nurseries in Wisconsin and Michigan or from reputable dealers is usually received in good condition. If the roots are kept moist and the trees are planted promptly, there should be little loss from poor stock. Careless planting can be reduced to a minimum by competent supervision and instruction of a planting crew by a man experienced in forest planting.

Planting Practice

White pine and white spruce are recommended as most desirable for planting on aspen sites. They may be planted either in the spring from the time the frost is out of the ground until June 1, or in the fall from about September 15 to the end of October. There are examples of spring and fall planting in the region, both showing excellent results.

Several classes of nursery stock of white pine, including 2-0, 3-0, 4-0, 1-2, 2-1, and 2-2,[6] have been tried. The 3-0, 1-2, and 2-1 may be recommended. The 3-0 stock is the least expensive of the classes that may be depended on to be satisfactory. In experiments at Cloquet, Minnesota (Hansen, 1927), 1-2 and 2-0 stock gave best results. In general, however, 2-0 stock must be of exceptionally high quality to give satisfactory results.

Transplant stock is generally considered essential with white spruce. White spruce planting on a large scale in Ontario, north of Sault Ste. Marie, on open sites cut over for pine and spruce 14 years before planting and badly burned since, has survived 83 to 85 per cent. The work was done by a private company, using 4-year-old transplant stock at a cost of about $12 per thousand trees planted.[7] This record is more favorable than is that of the earlier experience in Minnesota. Further experiments may demonstrate that 3-0 stock can be used. Lacking definite evidence, 2-1 or 2-2 stock of white spruce is recommended.

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[6] The first figure represents the number of years in the seedbeds; the second, years in the transplant beds. Thus, 3-0 is 3-year seedling stock.

[7] Information furnished through the courtesy of B. F. Avery, Forester of the Spanish River Pulp and Paper Mills.

Methods of planting.—Methods suitable for use in planting aspen lands may be grouped into two classes—slit and hole methods. In the hole method a hole large enough to hold the outspread roots of the tree is dug with a spade, mattock, or grub hoe, the tree is held in place, and the earth is filled in around the roots. Two men are ordinarily required, one to dig the holes and the other to set the trees and fill in the earth about the roots. The method is satisfactory almost any place where planting can be done. Objections to it are that it is slow and expensive and the earth has a tendency to settle and form depressions around the seedlings. These depressions, in underplantings of aspen, collect the aspen leaves, which may bury the seedlings.

The slit method consists in opening a slit with a spade or a special wedge-shaped planting iron with a handle. The roots of the tree are inserted in the slit and the opening about the roots is closed with another thrust of the blade. The man who makes the slit plants the tree. This method is rapid and inexpensive and has given satisfactory results. It is not adapted, however, to rocky or shallow soils. On these the hole method or direct seeding may have to be used. Detailed descriptions of the methods and tools, and directions for planting are given in several other publications (Cox, 1911, Hansen, 1927, Kittredge, 1928). Examples of highly successful plantations on aspen lands by both these methods or modifications of them in different parts of the Lake States testify to their usefulness.

In order to assure a good yield from the planted conifers, 500 to 800 trees to the acre, if possible, should be set out. This is less than is usually recommended for open sites, because in underplanting it is desirable to avoid placing the planted trees too close to large trees or clumps of brush already established. In dense stands of aspen, the number may have to be reduced to 300 or 400 to the acre. The planted trees should be spaced about 6 feet apart each way where brush and larger trees do not interfere. Obviously, in dense stands no uniform system of spacing can be followed. With 400 trees to the acre and allowing for a possible loss of 20 to 50 per cent during the early life of the plantation, more than 200 trees to the acre would be left. This should be sufficient to provide a good yield at maturity.

There are large areas of comparatively inaccessible stands of aspen that it will not be feasible to plant completely for many years and that have not enough coniferous seed trees to promise effective natural conversion. These areas may be converted gradually and at less cost by partial planting in strips or groups. Under one system the trees are planted in strips of 5 to 20 rows and an area of equal or greater width is left unplanted. Another strip of 5 to 20 rows is planted on the far side of the unplanted strip. In this way the cost of planting for the area as a whole may be reduced to half or less. These strips, in time, should form a stand of conifers sufficient to provide a merchantable crop. Before they are cut they may be expected to bear seed and reproduce naturally on the intervening unplanted strips. Incidentally, if the aspen is logged before the conifers are, the logging may be laid out so that most of the roads and skidding trails are in the unplanted strips, thus minimizing the damage to the conifers in the planted strips. The second system of partial planting may be called group planting. From 10 to 100 trees would be included in a group and the groups spaced 200 to 500 feet apart. The object and results of group planting would be similar to those for strip planting. If the groups were more widely spaced, the cost for the area could be reduced, with a correspondingly lower or longer deferred return from the planting.

Results in Plantations on Aspen Lands

Good survival has been obtained in a large proportion of the white pine and Norway pine plantations on aspen lands in Michigan and Wisconsin. The figures for Minnesota plantations are not quite so favorable because damage by rabbits has been much more severe here. The results are shown below in tabular form.

PERCENTAGE OF PLANTATIONS GROUPED ACCORDING TO SURVIVAL

Survival group	Survival per cent	White pine	Norway pine	Norway spruce
Good	60 or more	47	16	33
Medium	30 to 60	47	16	33
Poor	30 or less	10	10	34
Basis, number of plantations.......		40	19	6

The only one of the 19 Norway pine plantations with more than 0.45 crown density of aspen-birch had the lowest survival, 12 per cent. The three plantations of white spruce in Minnesota had 11, 24, and 32 per cent survival, respectively, and correspondingly poor growth owing largely to damage by rabbits. They should not, therefore, be considered representative of the results that may be expected with white spruce where it has a fair chance.

The average annual height growth in plantations 5 to 15 years old was 0.29 foot for white pine, 0.31 for Norway pine, and 0.28 for Norway spruce. The most rapid annual growth among the white pine plantations was 0.61 foot under 0.6 cover of aspen, and the best for Norway pine, 0.59 under 0.4 cover.

The results in existing plantations are not discouraging except in the brushy rabbit-infested areas of northern Minnesota.

Costs of Planting

The rate of planting aspen areas with white pine or white spruce, as already described, should be between 300 and 1,000 trees per man per day. Allowing $5.00 per 1,000 trees for the nursery stock and supervision, the total cost of planting 700 trees to the acre would be between $6.50 and $10. Thick brush or rocky sites might easily raise the cost to $15 or even $20 an acre. On the other hand, lower costs would be possible on sites easy to plant or if fewer trees to the acre were planted. It is estimated that a large proportion of the aspen lands could be planted for about $8.00 an acre.

ADVANTAGES OF ASPEN AND CONIFEROUS STANDS

Stands of aspen in the limited areas where it is marketable for $1.00 a cord or more, yield from 10 to 20 cords to the acre in 40 or 50 years. It may be expected, therefore, to return from 3 to 4 per cent compound interest on the investment and carrying charges. In other words, even the aspen that is favorably located will pay only a low profit as a timber growing enterprise. Low yields have been intentionally assumed in the foregoing statement to allow for the considerable areas where aspen stands are sufficiently open for the development of either natural or planted pine and spruce.

Pine and spruce under or mixed with the aspen will require from 60 to 100 years to become merchantable. They will, therefore, grow for 20 to 50 years after the aspen is cut. If the yield of 12 cords to the acre of white spruce at 100 years, previously quoted from Kenety (1917), is taken as an example, a calculation may be made of the advantages of natural conversion. Assuming taxes at 10 cents an acre and protection at 3 cents an acre, for a 50-year period after the aspen is cut, the spruce with a stumpage value of $6.05 per cord would earn 6 per cent on the investment, at $4.01 would earn 5 per cent, and at $2.67 would earn 4 per cent compound interest. The future values of spruce stumpage will almost certainly be as high as those indicated or higher, so the spruce resulting from the natural conversion of aspen will earn 5 or 6 per cent profit or more.

Under similar circumstances, white pine yielding 5,000 board feet to the acre would have to have stumpage values of $14.53 to earn 6 per cent, of $9.63 to earn 5 per cent, and of $6.42 to earn 4 per cent. Again, these values are hardly more than the present stumpage values of white pine in the region. There is, therefore, ample justification for fire protection and encouragement of timber growing on aspen areas with natural white spruce or white pine in the attractive returns to be anticipated from the spruce or pine even when they produce only conservatively low yields to the acre.

On the large areas where planting will be necessary, the prospect is less favorable. Planting may be expected to cost, on the average, $8.00 an acre. Again assuming that the aspen will carry the annual expenses for the first 40 or 50 years, there remain the charges for the 20 to 50 years after the aspen is cut and before the pine and spruce are merchantable, plus the interest on the planting investment of $8.00 an acre over the 60- to 100-year rotation of the pine or spruce. Planted stands of white pine on aspen areas may reasonably be expected to yield 10,000 board feet to the acre at 80 years, and 20,000 board feet at 100 years. The corresponding yields for white spruce would be 20 cords at 80 years and 35 cords at 100 years. The stumpage values that the pine or spruce would have to have under these conditions to earn different percentages on the costs and investment, are shown in the following table.

Interest, per cent	White Pine		White Spruce	
	Yields		Yields	
	10,000 board feet in 80 years	20,000 board feet in 100 years	20 cords in 80 years	35 cords in 100 years
	Future stumpage values			
6	$91.90	.....	$45.95	.....
5	48.46	$55.01	24.23	$31.43
4	21.65	21.80	10.82	12.46

The stumpage values are comparable with those in sales at the present time, only at 4 per cent interest. Greater returns are dependent on the possible speculative rises in stumpage values during the next 40 or 50 years, which are not impossible or even unlikely in view of the decreasing supply of spruce and white pine.

SUMMARY

To sum up, aspen grows rapidly and produces large volumes of wood in 40 to 50 years. It will probably return 4 to 5 per cent interest on the investment, even at very moderate stumpage prices, and it is easily managed. The aspen is therefore an excellent timber crop for an industry that can use it to advantage or for any owner so located that he can sell it readily. Few owners of aspen land, however, are now so situated.

The majority of owners, who can see no likelihood of using or selling their aspen and face the prospect that much of the oncoming crop will rot on their hands, should consider conversion to pine and spruce. The encouragement of natural conversion can almost always be justified on the ground of economic advantage and profit. Artificial conversion by planting, which involves an investment of $8.00 an acre, more or less, may return not more than 4 per cent on the investment. The planting is, therefore, advisable chiefly for public agencies and for private industries that need the pine or spruce and are willing to forego a high rate of interest on the timber-growing part of the business in order to maintain the manufacturing part and the higher profits derivable from it.

From the viewpoint of public welfare, a future supply of conifers is more needed than a supply of aspen. Conversion of aspen to conifers should, therefore, be encouraged, both by assistance to private owners of aspen lands in the conversion of their lands to conifers and by the initiation by public agencies of measures to promote the conversion on publicly-owned lands. On lands already publicly-owned, public agencies can well afford to invest funds in long-term timber-growing enterprizes that will yield 4 per cent. States, counties, and the federal government may also acquire additional aspen lands that would not otherwise be converted, as a partial solution of the problem.

What is the probable solution for the whole 21,000,000 acres of aspen-birch lands in the northern Lake States? Perhaps 20 per cent is being converted to conifers naturally. Possibly 30 per cent may be marketable for the aspen and birch on their own merits. It may be that 20 per cent of the area will be planted and converted by private owners during the next few decades, altho such a movement has hardly begun. The aspen on the remaining 30 per cent, including more than 6,000,000 acres, will deteriorate and go to waste unless steps are taken to prevent it. Two possible measures may be suggested: (1) The acquisition and planting of aspen lands by public agencies; (2) the dissemination of information as to the abundant supply of aspen, its value for present forms of utilization, and study of its properties for the purpose of developing new uses.

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APPENDIX

Volume Tables for Aspen and Paper Birch

TABLE XIII
Second Growth Aspen
(*Populus tremuloides* Michx.)
Minnesota

Gevorkiantz, S. R. 1926 Total cubic feet

Diameter breast high	Total height of tree—feet															Basis
	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	
Inches	Total volume—cu. ft.															Trees
2	.26	.31	.37	.42												31
3	.57	.69	.80	.92	1.0	1.1	1.3									74
4	1.0	1.2	1.4	1.6	1.8	2.0	2.2	2.4	2.6							84
5	1.6	1.9	2.2	2.5	2.8	3.1	3.4	3.7	4.0	4.3						74
6		2.7	3.1	3.5	4.0	4.4	4.9	5.3	5.8	6.2	6.6					61
7				4.8	5.4	6.0	6.6	7.2	7.8	8.3	8.9	9.5	10.1			42
8				6.2	7.0	7.7	8.5	9.3	10.0	10.8	11.6	12.4	13.1			47
9						9.7	10.7	11.6	12.6	13.6	14.5	15.5	16.5			38
10						11.9	13.1	14.3	15.4	16.6	17.8	19.0	20.2	21.4		36
11							15.7	17.1	18.6	20.0	21.4	22.9	24.3	25.7		24
12								20.2	21.9	23.6	25.3	27.0	28.7	30.4		27
13									25.6	27.6	29.6	31.6	33.5	35.5	37.5	23
14										31.9	34.1	36.4	38.7	41.0	43.3	18
15										36.4	39.0	41.6	44.2	46.8	49.4	5
16										41	44	47	50	53	56	
Basis	9	20	47	52	63	63	43	44	43	33	38	47	57	24	1	584

Volume includes stump, stem, and top without bark
Compiled by the form factor method from data collected by E. E. Probstfield in 1925.
Cubed in 8-foot sections by Smalian's formula. A. F. Verrall assisted in compilation.
Block indicates extent of original data.
Difference between total volume of trees used as a basis and volumes as taken from the table, +0.08 per cent.
Average deviation of individual tree volumes from interpolated tabular volumes, ±5.33 per cent.

TABLE XIV

SECOND GROWTH ASPEN
(*Populus tremuloides* Michx.)
Minnesota

Gevorkiantz, S. R.
1926
Merchantable cubic feet

Diameter breast high	Total height of tree—feet														Basis
	30	35	40	45	50	55	60	65	70	75	80	85	90	95	
Inches	Merchantable volume—cu. ft.														Trees
4	.58	.76	.93	1.1	1.3	1.5	1.6	1.9							84
5	1.3	1.5	1.8	2.2	2.5	2.8	3.1	3.4	3.7						74
6	2.2	2.5	2.9	3.4	3.8	4.2	4.7	5.2	5.6	6.1					61
7			4.2	4.8	5.4	5.9	6.5	7.2	7.8	8.4	8.9	9.5			42
8			5.6	6.3	7.0	7.8	8.6	9.4	10.2	11.0	11.7	12.5			47
9					8.9	9.9	10.8	11.8	12.8	13.8	14.8	15.8			38
10					11.0	12.2	13.4	14.6	15.8	17.0	18.2	19.4	20.6		36
11						14.7	16.2	17.6	19.1	20.5	22.0	23.4	24.9		21
12							19.2	20.9	22.6	24.4	26 1	27.7	29.5		27
13								24.5	26 5	28 5	30.5	32 4	34.4	36 4	21
14									30.7	33 0	35.2	37.5	39.8	42.1	18
15									35.1	37.7	40.2	42.8	45.4	48.0	5
16									40	43	46	49	52	55	
Basis		4	25	57	63	43	44	43	33	38	47	57	23	1	477

Volumes inside of bark.
Stump height, 1 foot; top diameter inside of bark, 3 inches.
Compiled by expressing merchantable volume as a percentage of the total volume.
Data collected in 1925 by E. E. Probstfield. A. F. Verrall assisted in the compilation.
Difference between total volume of trees used as a basis and volumes as taken from the table, —0.16 per cent.
Average deviation of individual tree volumes from interpolated tabular volumes, ±6.05 per cent.
Block indicates extent of original data.

TABLE XV

SECOND GROWTH ASPEN
(Populus tremuloides)
Minnesota

Gevorkiantz, S. R. 1926 International ⅛ inch kerf.

Diameter breast high	Number of 16-foot logs								Basis
	1	1½	2	2½	3	3½	4	4½	
Inches	Volume—bd. ft.								Trees
6	15	20	26	31					43
7	15	24	32	40					42
8	15	27	39	50	60				47
9	15	30	44	58	74	90			37
10		34	51	68	86	104	122		36
11		37	58	79	100	120	144	167	22
12		41	66	92	118	144	171	198	26
13			75	106	138	170	202	233	23
14			86	123	161	199	237	274	18
15				142	186	230	276	319	5
16				163	213	264	319	369	
Basis	36	36	32	35	44	39	68	9	299

Stump height, 1 foot; top diameter inside of bark, 5 inches; trees scaled in 16-foot lengths.

Compiled by the Frustum Form Factor method from data collected by E. E. Probstfield. A. F. Verrall assisted in the compilation.

Difference between total volume of trees used as a basis and volumes as taken from the table —0.13 per cent.

Average deviation of individual tree volumes from interpolated tabular volumes, ±5.33 per cent.

Block indicates extent of original data.

TABLE XVI
SECOND GROWTH ASPEN
(Populus tremuloides)
Minnesota

Gevorkiantz, S. R. 1926 Scribner Decimal C.

Diameter breast high	Number of 16-foot logs								Basis
	1	1½	2	2½	3	3½	4	4½	
Inches	Volume—bd. ft.								Trees
7	2	3	4	6					20
8	2	3	4	6	7				47
9	2	3	5	6	8	9			37
10		3	5	7	8	10	12		36
11		4	6	7	9	11	13	15	22
12		4	6	8	10	13	15	17	26
13			7	9	12	14	17	20	23
14			8	11	14	16	19	23	18
15				12	15	19	22	26	5
16				14	17	22	26	30	
Basis	22	34	27	45	25	45	35	1	234

Stump height, 1 foot; top diameter inside of bark, 6 inches. Scaled in 16-foot lengths.

Compiled by the Frustum Form Factor method from data collected in 1925 by E. E. Probstfield. A. F. Verrall assisted in the compilation.

Difference between total volume of trees used as a basis and volumes as taken from the table, +0.35 per cent.

Average deviation of individual tree volumes from interpolated tabular volumes, ±6.48 per cent.

Block indicates extent of original data.

TABLE XVII
ASPEN
(Populus tremuloides)
Minnesota

Gevorkiantz, S. R. 1928 Cords per tree

Diameter breast high	Total height of tree—feet														Cubic feet of wood per cord
	30	35	40	45	50	55	60	65	70	75	80	85	90	95	
Inches	Peeled volume—cords														
4	.010	.013	.016	.019	.022	.026	.028	.032							58
5	.021	.025	.028	.035	.040	.045	.050	.055	.030						61
6	.034	.039	.045	.053	.060	.066	.073	.081	.088	.095					64
7			.062	.070	.079	.087	.096	.11	.11	.12	.13				68
8			.078	.089	.099	.11	.12	.13	.14	.15	.16	.17			71
9					.12	.13	.14	.16	.17	.18	.20	.21			74
10					.14	.16	.17	.19	.21	.22	.24	.26	.27		76
11						.19	.21	.23	.25	.26	.28	.30	.32		78
12							.24	.26	.28	.31	.33	.35	.37		79
13								.30	.33	.35	.38	.40	.43	.45	80
14									.37	.40	.43	.46	.48	.51	82
15									.42	.45	.48	.51	.54	.57	84
16									.47	.51	.54	.58	.61	.65	85

Standard cords, 4x4x8 feet.
Volume of peeled stem above a one-foot stump to a top diameter inside of bark, 3 inches.
Compiled from the merchantable volume in cubic feet by dividing the volume per tree by the number of cubic feet per cord for each diameter.
Eleven stacks of closely piled wood were measured to establish the relation between cubic feet and cords.
Wood was cut in 8-foot lengths and piled. Converting factors, cubic feet per cord, give volume inside bark in each cord of unpeeled wood.
Basis was 477 trees distributed as in the table of merchantable cubic feet.
Block indicates extent of original data.

TABLE XVIII

SECOND GROWTH PAPER BIRCH

(Betula papyrifera)

Lake States

Gevorkiantz, S. R. 1926 Cubic feet

Diameter breast high	Total height of tree—feet										Basis
	25	30	35	40	45	50	55	60	65	70	
Inches	Total volume—cu. ft.										Trees
2	.28	.34	.40	.46	...	...	...	...	...	...	17
3	.61	.74	.86	.98	1.1	1.2	...	...	...	...	21
4	1.1	1.3	1.5	1.7	1.9	2.1	2.3	...	...	...	21
5	...	1.9	2.3	2.6	2.9	3.2	3.6	3.9	...	...	18
6	...	2.7	3.2	3.6	4.1	4.5	5.0	5.5	5.9	...	14
7	...	...	4.2	4.9	5.5	6.1	6.7	7.3	7.9	8.5	13
8	...	...	...	...	7.0	7.7	8.5	9.3	10.1	10.8	8
9	...	...	...	...	8.6	9.6	10.6	11.5	12.5	13.5	3
10	...	...	...	...	...	11.7	12.8	14.0	15.2	16.3	1
Basis	1	18	13	15	18	18	12	18	2	1	116

Volume includes stump, stem, and top without bark.

Compiled by the Form Factor method from data collected in 1926.

Cubed in 8.15-foot sections by Smalian's formula.

Block indicates extent of original data.

Difference between total volume of trees used as a basis and volumes as taken from the table, −0.06 per cent.

Average deviation of individual tree volumes from interpolated tabular volumes, ±4.01 per cent.

TALE XIX
Second Growth Paper Birch
(Betula papyrifera)
Lake States

Gevorkiantz, S. R. 1926 Merchantable cubic feet

Diameter breast high	Total height of tree—feet								Basis
	35	40	45	50	55	60	65	70	
Inches	Merchantable volume—cu. ft.								Trees
4	.69	.92	1 2	1.4	1.7				21
5	1 5	1 9	2.2	2.6	3.0	3.3			18
6	2.5	3.0	3.5	4.0	4.4	4.9	5.3		14
7	3 6	4.2	4.8	5.5	6.1	6.7	7.3	7.9	13
8		5.6	6.4	7.1	7.9	8.7	9.5	10.3	8
9			8.0	9.0	9.9	10.9	11.9	12.8	3
10				11.0	12.2	13.4	14.5	15.7	1
Basis	1	9	17	18	12	18	2	1	78

Volume inside of bark.

Stump height, one foot; top diameter inside of bark, 3 inches.

Compiled by expressing merchantable volume as a percentage of the total volume.

Data collected in 1926.

Difference between total merchantable volume of trees used as a basis and volumes as taken from the table, +0.19 per cent.

Average deviation of individual tree volumes from interpolated tabular volumes, ±7.7 per cent.

Block indicates extent of original data

TALE XX
Second Growth Paper Birch
(Betula papyrifera)
Lake States

Gevorkiantz, S. R. 1926 Cords

Diameter breast high	Total height of tree—feet								Basis
	35	40	45	50	55	60	65	70	
Inches	Peeled volume—cords								Trees
4	.01	.01	.02	.02	.02				21
5	.02	.02	.03	.03	.04	.04			18
6	.03	.04	.04	.05	.05	.06	.07		14
7	.04	.05	.06	.06	.07	.08	.09	.09	13
8		.06	.07	.08	.09	.10	.11	.12	8
9			.09	.10	.11	.12	.13	.14	3
10				.12	.13	.14	.15	.16	1
Basis	1	9	17	18	12	18	2	1	78

Standard cords, 4x4x8 feet.

Volume of peeled stem above a one-foot stump to a top diameter inside of bark, 3 inches.

Compiled from the merchantable volume in cubic feet by dividing the volume per tree by the number of cubic feet per cord for each D.B.H. class by the use of cordwood factors from U. S. Forest Service Circular 163 converted to D.B.H. basis.

Data collected in 1926.

Block indicates extent of original data.

Common and Scientific Names of Trees Mentioned in Text

Common Name	Scientific Name
American elm	*Ulmus americana*, Linnaeus
Aspen	*Populus tremuloides*, Michaux
Balsam fir	*Abies balsamea*, (Linnaeus) Miller
Balsam poplar	*Populus balsamifera*, Linnaeus
Basswood	*Tilia Glabra*, Ventenat
Black ash	*Fraxinus nigra*, Marshall
Black spruce	*Picea Mariana*, (Miller) Britton, Sterns, and Poggenberg
Bur oak	*Quercus macrocarpa*, Michaux
Eastern hemlock	*Tsuga canadensis*, (Linnaeus) Carriers
Green ash	*Fraxinus pennsylvanica lanceolata*, (Borkhausen) Sargent
Hop-hornbeam	*Ostrya virginiana*, (Miller) Koch
Jack oak	*Quercus ellipsoidalis*, E. J. Hill
Jack pine	*Pinus banksiana*; Lambert
Large-tooth aspen	*Populus grandidentata*, Michaux
Northern white cedar	*Thuja occidentalis*, Linnaeus
Northern white pine	*Pinus strobus*, Linnaeus
Norway pine	*Pinus resinosa*, Solander
Norway spruce	*Picea abies*, Karst
Paper birch	*Betula papyrifera*, Marshall
Pin cherry	*Prunus pennsylvanica*, Linnaeus fils
Red maple	*Acer rubrum*, Linnaeus
Red oak	*Quercus borealis*, Michaux
Red spruce	*Picea rubra*, Link
Scarlet oak	*Quercus coccinea*, Muenchhausen
Scotch pine	*Pinus sylvestris*, L.
Sugar maple	*Acer saccharum*, Marshall
Tamarack	*Larix laricina*, (DuRoi) Koch
Western white pine	*Pinus monticola*, D. Don
White spruce	*Picea glauca*; (Moench) Voss
Yellow birch	*Betula lutea*, Michaux

Common and Scientific Names of Shrubs and Herbaceous Vegetation Mentioned in the Text

Common Name	Scientific Name
Alder	*Alnus incana*, (L.) Moench.
Arbutus	*Epigaea repens*, L.
Bedstraw	*Galium boreale*, L.
Bellwort	*Uvularia grandiflora*, Sm.
Baneberry	*Actaea rubra*, (Ait.) Willd.
Blueberry	*Vaccinium pennsylvanicum*, Lam.
Brake fern	*Pteris aquilina*, L.
Canada mayflower	*Maianthemum canadense*, Desf.
Choke cherry	*Prunus virginiana*, L.
Clintonia	*Clintonia borealis*, Ait.

Clubmoss	*Lycopodium spp.*, not *complanatum,* L.
Dwarf raspberry	*Rubus triflorus,* Richards
Dogwood	*Cornus paniculata,* L'Her.
	Cornus circinata, L'Her.
Early meadow rue	*Thalictrum dioicum,* L.
Fern	*Asplenium filix-femina,* (L.) Bernh.
	Aspidium spinulosum, (O. F. Muller) Sw.
	Osmunda claytoniana, L.
Gooseberry	*Ribes spp.*
Ground pine	*Lycopodium complanatum* var. *flabelliforme,* Fernald
Hazel	*Corylus americana,* Walt.
	Corylus rostrata, Ait.
Hepatica	*Hepatica acutiloba,* DC.
Large leafed aster	*Aster macrophyllus,* L.
Mountain maple	*Acer spicatum,* Lam.
Mitrewort	*Mitella nuda,* L.
Pyrola	*Pyrola secunda,* L.
	Pyrola rotundifolia, Man. ed. 6, not L.
Raspberry	*Rubus idaeus* var. *aculeatissimus* (C. A. Mey) Regel and Tiling
Starflower	*Trientalis americana,* (Pers.) Pursh.
Sweet fern	*Myrica asplenifolia,* L.
Twisted-stalk	*Streptopus roseus,* Michx.
Viburnum	*Viburnum dentatum,* L.
	Viburnum opulus L. var. *americanum* (Mill) Ait.
Wild ginger	*Asarum canadense,* L.
Wintergreen	*Gaultheria procumbens,* L.

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CONTENTS

Page

Introduction 3

Aphids recorded on Rubus in North America 4
  Their synonomy and host plants 4

Aphids recorded on Rubus in Europe 9
  Their synonomy and host plants 9

Notes on the Biology and Morphology of *Amphorophora rubi* (Kaltenbach), *Amphorophora rubicola* (Oestlund), and *Aphis rubicola* (Oestlund) 11

Distribution and movement of wingless forms of *Amphorophora rubi* (Kaltenbach) 14
  Agencies of distribution 14
  Factors causing dislodgment from foliage 14
  Behavior when dislodged from foliage 16
  Distance and rate of movement on the ground 16
  Behavior when leaves become wilted 17

Resistance of the Herbert raspberry to *Amphorophora rubi* (Kaltenbach) 17
  Field counts of population on cultivated varieties 17
  Inability of *A. rubi* to maintain its population on Herbert 18
  Possible reasons for resistance shown by Herbert 23

Aphids recorded on Rubus arranged under their host plant species 25

Summary 37

Literature cited 28

ILLUSTRATIONS

Page

Fig. 1. Population of *A. rubi* on three varieties grown in the same container 20

2. Population of *A. rubi* on three varieties in separate containers 22

3. Population of *A. rubi* on Herbert and Latham when confined to individual containers 24

A PRELIMINARY ACCOUNT OF THE RASPBERRY APHIDS

J. D. Winter

INTRODUCTION

Aphids are mentioned frequently in published data as vectors of mosaic and other virus diseases. The data often show that a definite relationship exists between a specific virus and one or more species of aphid. For example, several species may occur on a given food plant but only one may be able to transmit a specific virus disease.

The writer became interested in the aphids of the bramble fruits because of the wide distribution of virus diseases in cultivated plantings of these fruits. Much investigational work on these diseases has been done in recent years. In the bramble fruits the injection of plant juices from diseased plants has failed to transmit virus infection. Inoculation has been successful only with the use of aphids as vectors.

A search of the literature failed to disclose any publication dealing with the bramble fruit aphids as a group, or giving a general survey of species and distribution. Only recently have these aphids been considered of economic importance and little work has been done with them from this viewpoint. An attempt has been made, therefore, to bring together a complete record of the bramble fruit aphids of North America and Europe, including their synonomy and host plant species.

The brambles, which comprise the genus Rubus, consist of many distinct forms and an almost endless number of intermediate forms. Much confusion and uncertainty in the taxonomy of this group are the result. Bailey (1916) states that more than 3,000 species have been named, of which at least 400 are well defined forms. The genus is widely distributed in North America, where at least 100 species have been described. The horticultural varieties grown in North America for their fruit are derived principally from American and European species of Rubus.

Grateful acknowledgment is made to Professor A. G. Ruggles, of the Division of Entomology and Economic Zoology, for his many helpful suggestions and his kindness in extending facilities for the work; to Dr. C. E. Mickel, of the same division, for advice and suggestions on various problems, especially those relating to taxonomy; and to Dr. O. W. Oestlund, of the Department of Animal Biology, for much kindly advice and assistance.

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APHIDS RECORDED ON RUBUS IN NORTH AMERICA

Their Synonomy and Host Plants

Ten species of aphids are recorded as feeding on Rubus in North America. Only five of these are of wide distribution—*Amphorophora rubi, Amphorophora rubicola, Amphorophora sensoriata, Aphis rubicola,* and *Cerosipha rubifolii.* The literature mentions *Aphis rubiphila* Patch as being of wide distribution, but the writer (1929) considers this aphid identical with *Aphis rubicola* Oestlund. The blackberry aphid, *C. rubifolii,* is usually the only species that causes any appreciable direct injury to the host plant.

The records of two species included—*Macrosiphum ambrosiae* and *Pemphigus rubi*—indicate the probability that they were accidentally on Rubus when collected. In the literature it is common to find aphid species described as living on certain host plants on the strength of limited observation, in some instances on the collection of a single specimen. The writer believes that many unwarranted conclusions are thus reached that would be disproved by further study. During this study 16 additional species were taken on Rubus. The tribes Macrosiphini, Aphidini, Callipterini, and Anoeciini were represented in these collections. These 16 species are apparently distinct and none agree with the description of any of the species heretofore recorded on Rubus in North America. With three exceptions, not more than one specimen of the same species was taken in four years. The writer considers these specimens as accidentally on Rubus when collected.

Only one species is common to both Europe and North America. With the exception of the questionable record of *Macrosiphum ambrosiae,* these aphids have not been recorded on any food plant other than *Rubus sp.* in North America.

Genus AMPHOROPHORA[1]

Amphorophora davidsoni Mason

Amphorophora rubi (Kaltenbach) Swain (not *rubi* Kaltenbach), Univ. Calif. Pub., Ent. vol. 3, no. 1, 1919, p. 54

Amphorophora davidsoni Mason, Proc. U. S. Nat. Museum, vol. 67, art. 20, 1925, p. 26

Mason (1925) describes this species and reports it taken in 1911 by Davidson, in California, on thimbleberry. This probably refers to *Rubus parviflorus* Nuttall, syn. *R. Nutkanus* Moc. Mason believes the specimens that Swain (1919) described as *rubi* Kalt. to be this species. Swain reports specimens taken occasionally on thimbleberry in California.

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[1] Mason (1925) has been followed with respect to the species included under the genus Amphorophora.

Amphorophora maxima Mason

Amphorophora maxima Mason, Proc. U. S. Nat. Museum, vol. 67, art. 20, 1925, p. 35

Mason (1925) describes this species from a single alate specimen and several nymphs taken in 1911 on salmonberry in California. The food plant referred to is probably either *Rubus spectabilis* Pursh or *R. parviflorus*. The specimens were taken in August and constitute the only record of this species.

Amphorophora reticulata Mason

Amphorophora reticulata Mason, Proc. U. S. Nat. Museum, vol. 67, art. 20, 1925, p. 51

Mason (1925) describes this species from one alate viviparous female taken by Pergande, July, 1907, on raspberry in Washington, D. C. This species is distinguished from *A. rubi* by its smaller size; by the longer antennae, which are dark colored and more than twice as long as the body; by the cornicles, which are very distinctly reticulate at the tip; and by the fewer number of sensoria (20 on the specimen described) on antenna III.

Amphorophora rubi (Kaltenbach)

Aphis rubi Kaltenbach, Monographie der Familien der Pflanzenlause, 1843, p. 24

Siphonophora rubi (Kaltenbach) Koch, Die Pflanzenlause Aphiden, 1854, p. 191

Nectarophora rubi (Kaltenbach) Oestlund, Minn. Geol. and Nat. Hist. Surv. Bull. 4, 1887, p. 87

Macrosiphum rubi (Kaltenbach) Del Guercio, Nuove Rel. Staz. Firenze, ser. 1, no. 2, 1900, p. 159

Amphorophora rubi (Kaltenbach) Schouteden, Mem. de la Soc. Ent. de Belg., vol. 12, 1906, p. 242

Eunectarosiphon rubi (Kaltenbach) Del Guercio, Redia, vol. 9, 1913, p. 188

Rhopalosiphum rubi (Kaltenbach) Van der Goot, Beit. kennt. der Holland, Blattlause, 1915, p. 153

Acyrthosiphon (*Amphorophora*) *rubi rubi* (Kaltenbach) Mordvilko, Fauna de la Russie, 1919, p. 251

Nectarosiphon rubi (Kaltenbach) Patch, Conn. St. Geol. and Nat. Hist. Surv. Bull. 34, 1923, p. 310

Amphorophora rubi (Kaltenbach) Mason, Proc. U. S. Nat. Museum, vol. 67, art. 20, 1925, p. 52

This appears to be the most widely distributed of all aphids recorded on Rubus and is the only species common to both Europe and North

America. It is found on the leaves and canes of Rubus throughout the summer. The following food plants are recorded for this species:

Rubus caesius Linn. Kaltenbach 1843
Rubus corylifolius. Kaltenbach 1843
Rubus discolor. Kaltenbach 1843
Rubus fruticosus Linn. Kaltenbach 1843, Buckton 1876, Theobald 1917
Rubus idaeus Linn. Kaltenbach 1843, Buckton 1876, Theobald 1917
Rubus loganbaccus Bailey. Davidson 1912
Rubus occidentalis Linn. Gillette 1911, Guyton 1924
Rubus parviflorus Nutt. Davidson 1914 syn. *R. Nutkanus* Moc.
Rubus saxtalis Linn. Patch 1918
Rubus strigosus Michx. Oestlund 1886, Patch 1914
Rubus vitifolius Ch. and Schl.[2] Essig 1917
Blackberry. Thomas 1879
Blackberry, cultivated. Essig 1917, Shinji 1917, Davidson 1912
Blackberry, wild. Shinji, 1917
Cytisus scoparius Link. Buckton 1876 syn. *Sarothamus scoparius* Wim.
Epilobium montanum Linn. Davidson 1925
Geum urbanum Linn. Davidson 1925

Mason (1925) believes that *Macrosiphum fragariellum* Theobald is identical with *A. rubi* Kalt., altho stating that Mordvilko considers it a subspecies, *A. rubi fragariellum.* Theobald (1926) states that *fragariellum* is common in Europe and lives entirely on the strawberry, the eggs being found on that plant. Mason includes a translation of Mordvilko's key, which separates *rubi* into four subspecies. Two of these subspecies, *rubi amurense* and *rubi zhuravlevi,* are considered distinct species by Mason. According to Laing, Buckton's material collected on *Sarothamus scoparius* is the species *pisi.* Theobald (1926) says that the species taken by Walker on *Geum urbanum* is *gei* Koch, and believes that *rubi* feeds only on *Rubus sp.* In North America, *rubi* has not been taken on any food plant other than *Rubus sp.*

Amphorophora rubicola (Oestlund)

Macrosiphum rubicola Oestlund, Minn. St. Geol. Rept. 14, 1886, p. 27
Nectarosiphon rubicola (Oestlund) Kirkaldy, Canad. Ent., 1906, p. 12
Nectarosiphum rubicola (Oestlund) Essig, Univ. Calif. Pub. Ent., vol. 1, no. 7, 1917, p. 329

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[2] Essig records the specimens taken on wild blackberry (*R. vitifolius*). As *R. vitifolius* is a dewberry, this record perhaps should be listed under blackberry.

Amphorophora rubicola (Oestlund) Davidson, Jour. Econ. Ent., 1914, p. 136

This species is widely distributed in North America. It is not believed to have an alternate host plant. The following food plants are recorded:

Rubus occidentalis Linn. Guyton 1924
Rubus parviflorus Nutt. Essig 1917, Swain 1919
Rubus strigosus Michx. Oestlund 1886, Patch 1914

Amphorophora sensoriata Mason

Amphorophora sensoriata Mason, Proc. Ent. Soc. Wash., vol. 25, no. 9, 1923, p. 188

This species is widely distributed in North America on the black raspberry but is not often found on the red raspberry. It has been taken occasionally by the writer on black raspberry in Minnesota, where it occurs in strong colonies that feed on the terminal leaves and canes. This aphid is readily distinguished from *rubi* and *rubicola* by the shorter cornicles and the more numerous sensoria in both alate and apterous forms. It has been collected on Rubus throughout the growing season and is believed not to have an alternate host plant. Dr. C. W. Bennett, in a letter to the writer, states that this species has appeared every season for three years in cages where only raspberries and a small amount of June grass were present.

GENUS APHIS

Aphis rubicola Oestlund

Aphis rubicola Oestlund, Minn. Geol. and Nat. Hist. Survey, Bull. 4, 1887, p. 60
Aphis rubiphila Patch, Maine Agr. Exp. Sta. Bull. 233, 1914, p. 269

This species is recorded as common on the red raspberry and is widely distributed in North America. Swain (1919) states that Davidson, in 1916, found specimens believed to be *rubicola* on loganberry and blackberry in California. The writer has collected this species on cultivated black raspberry.

GENUS CEROSIPHA

Cerosipha rubifolii (Thomas)

Sipha rubifolii Thomas, 8th Rept. State Ent. Ill., 1879, p. 121
Cerosipha rubifolii (Thomas) Davis, Jour. Econ. Ent. vol. 3, 1910, p. 492
Aphis rubi Bennett, Mich. Agr. Expt. Sta. Tech. Bull. 80, 1927, p. 14

This is the common blackberry aphid and is widely distributed on the blackberry in North America. It causes a characteristic curling of the foliage, particularly on the young leaves near the tips of the canes. Sanborn (1904) reports this species on the cultivated blackberry in Kansas; Davis (1910), on the wild and cultivated blackberry in Illinois; Baldwin (1912), on the wild blackberry in Indiana; and Guyton (1924), on the blackberry in Ohio. This species has not been recorded from Minnesota altho it is probably present but has been confused with *Aphis rubicola.* Wilson and Vickery (1918) list *Rubus occidentalis* and *R. villosus* as food plants of this species. *R. villosus* is probably the cultivated blackberry mentioned by Sanborn and others.

The writer observed that the published descriptions of this species coincided wtih the description of *Aphis rubicola* except that the antennae of *rubifolii* have only five segments. The location of the primary sensoria indicates that segments III and IV are merged. Upon inquiry, the writer found that there are no slides of *rubifolii* in the Thomas collection with the State Natural History Survey at Urbana, Illinois. Undoubtedly the type for this species is lost. A slide containing three alate viviparous females was kindly loaned to the writer by Dr. T. L. Guyton. These specimens were compared with *rubicola* and found apparently identical in every respect with the exception of the merged antennal segments. Dr. C. W. Bennett, who has worked with aphids in the transmission of virus diseases, states, in a letter to the writer, that *rubicola* usually will not satisfactorily live and reproduce on any variety of blackberry that he has worked with, while no difficulty is found in this respect with the common blackberry aphid. The blackberry aphid referred to by Bennett (1927) as *Aphis rubi* is undoubtedly *rubifolii,* altho no material is available for examination. This indicates strongly that *rubicola* and *rubifolii* are distinct species.

GENUS MACROSIPHUM

Macrosiphum ambrosiae (Thomas)

Siphonophora ambrosiae Thomas, Ill. State Nat. Hist. Bull. 2, 1878, p. 4

Nectarophora ambrosiae (Thomas) Oestlund, Geol. and Nat. Hist. Surv. Minn. vol. 4, 1887, p. 84

Macrosiphum ambrosiae (Thomas) Cockerell, Canad. Ent. vol. 36, 1904, p. 262

Tritogenaphis ambrosiae (Thomas) Oestlund, 19th Rept. State Ent. Minn. 1922, p. 142

Macrosiphum ambrosiae (Thomas) Soliman, Univ. Calif. Pub. Ent., Bull. 4, no. 6, 1927, p. 110

Thomas, in his original description of this species, records it from Iowa on *Ambrosia psilostachya* DeCand. Sanborn, in his Kansas Aphididae, records it on white snakeroot, *Eupatorium ageratoides.* Oestlund (1887) reports it common on *Ambrosia trifida* Linn. Gillette

(1911) reports it abundant on this food plant and also taken on *Iva xanthifolia* and *Rudbeckia sp.* Swain (1919) reports what was probably this species on *Helianthus annus* Linn. Davis (1913) remarks that this species may be identical with *M. rudbeckiae* Fitch. Soliman (1927) states that the species recorded by Sanborn is not *M. ambrosiae* (Thomas). No mention is made by these authors of this aphid occurring on Rubus. Wilson and Vickery (1918) record this species on *Rubus villosus*. Owing to the meager records of this aphid on Rubus, it appears probable that its occurrence on Rubus was accidental.

Genus PEMPHIGUS

Pemphigus rubi (Thomas)

Pemphigus rubi Thomas, 8th Rept. State Ent. Ill., 1879, p. 147

Thomas, in his original description, reports this species on the under side of leaves of *Rubus occidentalis* in Illinois. He states that the specimens may have been accidentally on the raspberry and that they closely resemble specimens found on *Populus tremuloides,* probably *Pemphigus populicaulis* Fitch. No winged forms were found. Davis, in his list of the Aphididae of Illinois, in 1910, states that there is no reference to the collection of this species since the original description by Thomas. It appears probable that Rubus is not a normal food plant for this aphid. Davis (1913) gives a further description of the Thomas specimens, with figures.

APHIDS RECORDED ON RUBUS IN EUROPE

Their Synonomy and Host Plants

Six species of aphids are definitely recorded as feeding on Rubus in Europe. Six additional species have been mentioned but the available records indicate that these six species do not feed normally on Rubus. Only one of the aphids found in Europe has been recognized in North America.

Genus AMPHOROPHORA

The only species of Amphorophora recorded in Europe is *Amphorophora rubi* (Kalt.). This species is widely distributed in Europe and in North America. The synonomy and list of host plants are given under the species found in North America.

Genus APHIS

Aphis idaei Van der Goot

Aphis idaei Van der Goot. Tijdschr. voor Ent. 55, 1912, p. 78

According to Davidson (1925) this species is recorded several times on *Rubus idaeus* in Europe. Van der Goot records finding it on *Rosa sp.*

Aphis mordwilkiana Dobrowljansky

Aphis mordwilkiana Dobr. Kiev. Ent. Sta. South-Russian Agr. Syndicate, 1913, p. 34

According to Wilson and Vickery (1918), this aphid is recorded on *Rubus sp.* This is the only food plant recorded.

GENUS MACROSIPHUM

Macrosiphum poae (Macchiata)

Siphonophora poae Macchiati, Bul. Soc. Ent. Ital., 17, 1885, p. 62
Macrosiphum poae (Macchiati) Wilson and Vickery, Tr. Wisc. Acad. Sci., 19, pt. 1, p. 132

According to Wilson and Vickery (1918), this species is reported on *Rubus idaeus, Bromus sterilis* Linn., and *Poa annua* Linn.

Macrosiphum rubiellum Theobald

Macrosiphum rubiellum Theobald, Jour. Econ. Biol., 8, 1913, p. 147

Theobald (1926) states that this species is found on blackberry and raspberry until July, when alatae appear and migration occurs. He states that it apparently migrates to several alternate host plants, but species of *Galium* seem to attract it most. He records this aphid in England on *Rubus fruticosus, R. idaeus, Galium aparine,* and *Galium sp.*

Macrosiphum rubifolium Theobald

Macrosiphum rubifolium Theobald, Ent. vol. 50, 1917, p. 78

Theobald (1917) describes this species and records it in England on *Rubus fruticosus* and *Rubus idaeus.* Theobald (1926) mentions that this species bears a strong structural resemblance to *M. rosae.* He also states that Buckton's *Macrosiphum chelidonii,* which Buckton recorded on raspberry, is not Kaltenbach's *chelidonii* but is apparently *rubifolium.*

Other Aphids Mentioned as Feeding on Rubus

Buckton (1876) records *Macrosiphum cyparissiae* Koch on *Rubus sp.* Theobald (1926) states that Buckton's slide is in poor condition but that it looks like *M. rubifolium.* Wilson and Vickery (1918) list *cyparissiae* as feeding on *Rubus sp.* and other plants.

Wilson and Vickery (1918) list *Macrosiphum funesta* (Macchiati) as questionable on *Rubus idaeus.* This is the only food plant listed.

Buckton (1876) records *Macrosiphum chelidonii* (Kalt.) on raspberry, but Theobald (1926) states that the species recorded by Buckton on Rubus is apparently *M. rubifolium.* Wilson and Vickery (1918) and Davidson (1925) list *chelidonii* as feeding on *Rubus sp.*

Patch (1918), Wilson and Vickery (1918), and Davidson (1925) list *Hyalopterus trirhoda* (Walker) as feeding on *Rubus sp.* and other plants. Theobald (1926) does not include *Rubus sp.* as a food plant for this aphid.

Wilson and Vickery (1918) and Davidson (1925) list *Aphis urticaria Kalt.* as feeding on *Rubus sp.* Theobald (1926) states that this species has been confused with *Aphis idaei* with reference to the specimens collected on Rubus.

Davidson (1925) lists *Aphis urticae* Fabr. as feeding on *Rubus sp.* and other plants. Theobald (1926) mentions that it is impossible to determine the identity of this species described by Fabricius in 1775, altho the *urticae* Fabr. recorded by Roberts in 1915 is *urticaria* Kalt.

NOTES ON THE BIOLOGY AND MORPHOLOGY OF AMPHOROPHORA RUBI (KALTENBACH), AMPHOROPHORA RUBICOLA (OESTLUND), AND APHIS RUBICOLA OESTLUND

Amphorophora rubi (Kaltenbach)

This large-bodied species is the most active of the raspberry aphids found in Minnesota. When disturbed it moves readily and sometimes drops to the ground. Fluctuations in population are great, as might be expected, owing to the rapid rate of reproduction and the defenceless nature of the aphid against various enemies and unfavorable climatic conditions. After a period of hot, dry weather this aphid is often difficult to find in cultivated plantings. At other times large numbers may be found. In plantings where this species was unusually abundant, counts at various times averaged from 10 to 15 aphids per leaf, the leaves being selected at random from the tip of the canes. The abundance of this species is not correlated with the season of the year. Counts made in certain plantings about August 15, 1925, averaged as high as 14 aphids per leaf, altho they are usually not abundant in August.

In Minnesota this aphid is commonly found in plantings of cultivated red raspberry, but is not infrequent on the wild red raspberry and has been noted occasionally on the black raspberry and the cultivated dewberry. The favorite feeding place is the under side of the young leaves at the tip of the canes. Sometimes they feed directly on the young canes. It is not found in colonies as is *Amphorophora rubicola.*

Winged forms are not common in Minnesota in summer. They have been taken from time to time in June, July, August, September, and October, the latest record being November 1, at University Farm in 1928. Apterous forms are common on the raspberry throughout the growing season, viviparous females being taken as early as June 15 at

Lake City in 1928. Alate males were taken on wild red raspberry at La Crescent on October 7, 1926, and in the greenhouse during the last half of October, 1928. Oviparous females were taken on cultivated red raspberry at Wayzata on October 16, 1925, at Byron on October 18, 1928, and in the greenhouse in the last half of October, 1928.

The eggs are not laid in large numbers and are difficult to find. Apterous viviparous females were reared from eggs on the canes of cultivated red raspberry collected at Duluth on May 5, 1927. On October 12, 1928, oviparous females were observed depositing eggs on some cultivated red raspberries being grown in the plant pathology greenhouse at University Farm. The majority of eggs were deposited on the under side of the leaves, altho a careful search revealed an occasional egg on the cane. Many alate males were found at the same time.

On October 13, 1928, three oviparous females were taken and placed in separate shallow glass containers with fresh raspberry leaves. The tops of the containers were covered with cheese-cloth and the leaves were kept properly moistened. Observation showed that the eggs were produced singly and at a slow rate. One individual died after the production of one egg; the other two each produced six eggs at an average interval of 7 to 11 hours, as shown in Table I.

TABLE I

Oviposition of Two Specimens of *Amphorophora rubi*

1928	No. 1	No. 2
Oct. 13, 4:00 p.m.	1st egg deposited	
" 14, 10:00 a.m.	2d and 3rd eggs found	
12:00 noon		1st egg deposited
7:00 p.m.	4th egg found	2d egg found
" 15, 10:00 a.m.	5th egg found	3rd and 4th eggs found
2:30 p.m.		5th egg deposited
" 15, 9:00 a.m.	6th egg found	6th egg found
" 18	Both aphids died	

The eggs were greenish white when deposited. The first eggs began to turn black at 4:00 p.m., October 17, and were completely black by noon of October 20, at which time they measured 0.67 to 0.76 mm. in length and 0.30 mm. in width. By November 1 they had shrunk slightly, measuring 0.65 to 0.70 mm. x 0.27 mm.

Amphorophora rubicola (Oestlund)

Mason (1925) records this species taken in March, April, and May in California; in July in Minnesota, British Columbia, and at Ottawa, Canada; in August in Maine; in October in Ontario. Oestlund mentions finding this species in Minnesota as late as November 1. The writer has taken alate and apterous forms in Minnesota throughout the growing season, from June to October. In 1925, alate males were taken as early as September 15 in the vicinity of Duluth on the wild red raspberry. There are no published records that the eggs have been observed.

In Minnesota this aphid is found most commonly on the wild red raspberry in the northern part of the state, where it is often abundant. It is not often found in cultivated plantings. Winged forms are more often seen than are winged forms of *rubi*. This aphid is readily distinguished from *rubi* by exceptionally long cornicles, which are decidedly longer than segment III of the antenna. Also by the conspicuous dusky spot at the tip of the front wings. In contrast to *rubi* it is markedly gregarious, and strong colonies are often found on the under side of leaves and on the canes near the tip of the new growth.

In describing the alate male, Mason (1925) had only one specimen, which had lost one antenna and all but part of segment III of the other. The antenna of the alate male is decidedly longer than the body and is dark colored except at the base of III. Antenna III is obviously shorter than the cornicles, with 50 to 60 circular sensoria; IV has none; and V has 8 to 10 sensoria.

Mason (1925), who apparently had only two specimens for observation, states that the apterous viviparous female has 13 to 15 sensoria on the basal half of III. The writer found that the sensoria on III varied from 7 to 17 in number and that they often extended somewhat beyond the basal half.

Aphis rubicola Oestlund

This species is readily distinguished by its small size from other aphids common to the raspberry in Minnesota. It is widely distributed on both wild and cultivated plants but appears to reach its greatest abundance on the wild red raspberry, *Rubus strigosus*. Observations made at Two Harbors, on September 12, 1925, where this species was unusually abundant, showed a maximum of 219 on a single leaf of the wild red raspberry. Twenty leaves taken at random averaged 54.7 per leaf.

This aphid is found on the under side of the leaves of red and black raspberries. It is not active and moves very little so long as the portion of the plant on which it is present remains suitable for food. Winged forms sometimes are quite numerous during the summer. Apterous forms are found on the raspberry throughout the growing season, from June to October. A decided preference is shown for certain cultivated varieties of the red raspberry, particularly Cuthbert, Golden Queen, and Sunbeam, according to field counts made at various times where several varieties were grown in adjoining rows.

Eggs of this species were collected in the spring of 1925 on cultivated red raspberry at Red Wing and were reared for identification, alate viviparous females being obtained. Canes of the wild red raspberry covered with enormous numbers of the eggs were collected on May 5, 1927, near Duluth. Specimens of this lot also were reared for identification. It is not usual to find eggs in such quantities, not more than one to six being generally found around each bud. The eggs are shiny black and are found on the cane mostly in the axils of the leaves. They are well hidden in the crevice formed by the bud except when they are numerous and are found on other portions of the cane. The eggs collected in the spring measure 0.43 to 0.49 mm. in length and 0.22 mm. in width. They begin to hatch when the buds first show green.

DISTRIBUTION AND MOVEMENT OF WINGLESS FORMS OF AMPHOROPHORA RUBI (KALTENBACH)

The distribution and movement of wingless forms of *Amphorophora rubi* are of special importance because winged forms are not abundant during the summer months and this species is known to be the principal vector of the mosaic group of virus diseases of bramble fruits. The distribution of wingless forms is limited by the distance they may be able to crawl or may be carried by some agency.

Agencies of Distribution

The possible agencies of distribution from plant to plant or from one planting to another are rain, wind, animals, birds, and persons, and equipment for the care and culture of raspberry plantings. No data are available on the possible distribution of *rubi* by animals or birds, but these factors are probably of little consequence. Wind is not likely to be an important factor in the distribution of wingless forms from one planting to another. The writer is informed by F. M. Wadley, J. E. Dudley, Jr., and others who have used tanglefoot screens extensively, that wingless aphids are usually not taken on these screens except close to the ground. It is possible that leaves bearing aphids occasionally may be carried a considerable distance by strong winds. Aphids may be carried on plants or plant parts removed from a planting or taken from one place to another. Observations show that *rubi* is frequently carried on the clothes of berry pickers and other workers who come in close contact with bushes on which this aphid is abundant.

Factors Causing Dislodgment from Foliage

Rankin (1927) found that rains may dislodge large numbers of *rubi* but that after rains of short duration they soon return to the bushes. It is probable that strong winds will dislodge some of them, altho no data on this point were obtained.

To determine whether aphids are dislodged when the foliage is disturbed, a white sheet was spread under individual bushes and a single-tree, such as is used with a cultivator, was brushed past the bush, approximately as if a horse cultivator were passing down a narrow row. The plants used were two years old in a planting of red raspberry at Nevis. A considerable number of *rubi* were found, but no data were obtained as to the number on each bush. Forty aphids were dislodged from the 10 bushes used in this experiment, as shown in Table II.

TABLE II
Dislodgment of *A. rubi* when Foliage is Disturbed

Date	Number of bushes	Number of aphids dislodged			
		Maximum	Minimum	Average	Total
July 19, 1926	10	10	0	4	40

To determine whether aphids are dislodged when a plant is removed by digging, 8 bushes were surrounded with a white sheet on July 20 and 21, 1926, at Nevis. The canes were cut off at the surface of the ground with a pair of pruning shears and were placed on the sheet as they were cut. The canes were handled in approximately the same way as when a plant is dug. As soon as all canes were cut they were lifted from the sheet and carried away. Forty-two aphids were found on the sheet and 189 on the foliage of the canes carried away. This indicates that in the ordinary process of roguing all the aphids are not removed with the rogued plant. The maximum temperature in the shade at the time of this experiment was 29 degrees C.; the minimum 20 degrees C.

Behavior When Dislodged from Foliage

To determine the behavior of *rubi* when dislodged and thrown to the ground, many individuals were studied. Adult forms were very active and crawled from 4 to 5 feet in 8 to 15 minutes. They will ascend anything in their path—a dead twig, a toothpick, the stem of a weed, a raspberry cane, or similar material. If it is something upon which they can not feed, they crawl down and proceed on their way. If it is a living raspberry cane with foliage they will invariably remain and feed. They appear to have no sense of direction or attraction toward raspberry canes that may be close at hand. This behavior probably explains why the virus infection that *rubi* is known to transmit spreads mostly to adjoining plants rather than at random through a planting. Aphids feeding on an infected plant, if disturbed and thrown to the ground, will either return to the same bush or will ascend the first bush in their path rather than pass through adjoining bushes to more distant ones.

Distance and Rate of Movement on the Ground

The distance that wingless forms are able to crawl from one planting to another is limited by the activity of the aphid and by the time it can live without food, if we assume that no plants of the genus Rubus exist at intermediate points. On three occasions adult and partly grown *rubi* were confined in glass containers covered with cheese-cloth, with paper substituted for raspberry leaves. The maximum time that they were able to live without food was 50 hours. Most of them survived 40 to 50 hours, the average being about 45 hours. Similar containers with raspberry leaves kept properly moistened were used as checks, the majority of aphids being alive at 100 hours in each experiment.

The following experiment was made at Nevis on July 19 and 20, 1926, to determine the distance covered by the wingless forms of *rubi* in a given time on cultivated ground. Sixteen adults were carefully placed on the ground between two rows of raspberry plants. Their distance in a straight line from the starting point was recorded at stated intervals, no account being taken of backward and wandering movements. The sixteen aphids traveled 428 inches in 120 minutes, averaging 3.6 inches each per minute. The maximum time one individual was under observation was 30 minutes and the distance traveled was 63 inches. The maximum distance traveled by one individual was 86 inches in 26 minutes. The temperature in the shade during this experiment ranged from 38 degrees to 43 degrees C. It is found that under favorable conditions the average time an aphid can exist without food is about 45 hours. Therefore the average theoretical distance that it would be capable of traveling is 810 feet. Actually, the distance it is likely to travel is probably much less because of other factors such as obstructions, storms, heat, and the improbability that one would travel continuously and in a relatively straight line for a long time.

The data on dislodgment, distance, and rate of travel of *rubi* indicate that movement of wingless forms from one planting to another is not likely to occur if such plantings are a relatively short distance apart. It was found that distribution within a planting occurs when the foliage is disturbed by cultural operations and by digging of plants, and that this species may be carried on the clothes of persons from one planting to another. Citations are given to show that rain and wind may be factors of distribution within a planting but not from one planting to another.

Behavior When Leaves Become Wilted

The following experiment was made at Nevis in 1926 to discover the behavior of wingless forms of *rubi* feeding on plants that are dug and left on the ground. Ten leaves with aphids feeding upon them were picked and placed on the ground. Care was taken to select aphids that were actually feeding and to disturb them as little as possible. Adult aphids were used except where noted. The data in Table III indicate that dispersal occurred as soon as the leaves began to wilt.

TABLE III
Behavior of *A. rubi* when Leaves Become Wilted

Date commenced, 1926	Hour	Temperature in shade	Condition of leaves	Position of leaves	Aphids present
July 18	6:30 p.m.	30° C.	just picked	in shade	10
	8:00 p.m.		not wilted	"	9
	9:00 a.m.		wilted	"	0
" 19	11:00 a.m.	32° C.	just picked	in sun	10
	12:00 noon		partly wilted	"	2
	3:00 p.m.		wilted	"	0
" 19	11:00 a.m.	32° C.	just picked	"	42*
	12:00 noon		partly wilted	"	0
" 19	5:00 p.m.	33° C.	just picked	in shade	40
	6:15 p.m.		slightly wilted	"	28
	9:00 a.m.		wilted	"	0
" 20	8:30 a.m.	25° C.	just picked	"	16
	9:30 a.m.		not wilted	"	14
	11:30 a.m.		partly wilted	"	6
	4:00 p.m.		wilted	"	0

* Nymphs.

RESISTANCE OF THE HERBERT RASPBERRY TO AMPHOROPHORA RUBI (KALTENBACH)

According to Darrow (1920), most of the red raspberries cultivated in North America are derived from the native American red raspberry, *R. strigosus,* or from hybrids between this species and the European red raspberry, *R. idaeus.* Darrow presents evidence to show that the varieties Cuthbert, Golden Queen, and Herbert are derived from *R. strigosus* x *R. idaeus* and that the variety King is derived directly from *R. strigosus.*

It is well known that raspberry varieties differ materially in their susceptibility to virus disease infection. Casual observation showed that *rubi* seemed to have a decided preference for certain varieties, indicating the possibility of correlation between virus susceptibility and host plant resistance.

Field Counts of Population on Cultivated Varieties

To secure data on the subject of host plant resistance, field counts were made in 1927 and 1928 in plantings where several cultivated varieties were grown in adjoining rows. The counts were taken on 100 leaves of each variety selected at random from the top of the canes. The leaves were taken from about 75 feet of continuous row of each variety and mostly in the same plantings throughout the two years.

The data in Table IV indicate a consistent relation between aphid population and the host plant variety. Herbert appears extremely resistant to *rubi* altho it is of interest to mention that this does not apply to *Aphis rubicola*, which was often found but is not abundant on this variety. Cuthbert and Golden Queen appear to be intermediate in resistance between Herbert and the other varieties. At Howard Lake, the Herbert was grown between Latham and Golden Queen in adjoining rows. At Lake City, the Herbert was between Cuthbert and St. Regis. The counts on Herbert were checked several times by counting an additional 100 leaves, but no more aphids were found than in the original count.

TABLE IV

NUMBER OF *A. rubi* ON 100 LEAVES SELECTED AT RANDOM

Variety	Eveleth	Howard Lake			Lake City		
	Aug. 3, 1928	July 26, 1927	Aug. 26, 1927	Aug. 18, 1928	July 23, 1928	Aug. 22, 1928	Sept. 16, 1928
Latham	92	75	38	21	227	27	12
King	..	84	29	19	280	40	16
Cuthbert	..	11	9	9	73	6	0
Golden Queen	..	6	11	18	70	4	3
Herbert	0	0	0	0	1	1	0
St. Regis	..	82	30	20	201	50	16
Sunbeam	..	82	21	28	..	..	..
June	66	..	..	..	..	..	..
Ontario	70	..	..	..	..	..	..

Comparison of Counts at Howard Lake and Lake City

Variety	Total leaves	Total aphids	Aphids per 100 leaves
King	600	468	78.0
Latham	600	400	66.7
St. Regis	600	399	66.5
Sunbeam	300	131	43.7
Golden Queen	600	112	18.7
Cuthbert	600	108	18.0
Herbert	600	2	0.3

Inability of A. rubi to Maintain Its Population on Herbert

To obtain further evidence on the relation between aphid population and the host plant variety, experiments were performed using potted plants of the varieties Herbert, King, and Latham of approximately the same size and in the same condition. These pots were kept in moist sand on a bench in the outdoor insectary at University Farm. Four-inch pots were used. Street-light globes large enough to hold three four-inch pots were used to separate the various lots. The tops were covered with a double thickness of cheese-cloth and the bottoms were embedded in the sand.

On July 30, 1928, one plant of Herbert, one of King, and one of Latham were placed under each of three of these globes. All aphids were removed, then six adult *rubi* were placed on each plant. A count of the leaflets over one-half inch in length on August 10 showed: Herbert 90 leaflets, Latham 78, and King 58, indicating that more feeding surface was available on the Herbert than on either of the other varieties. The plants were so placed in each container that their leaves intermingled, affording easy passage of the aphids from one plant to another. The *rubi* on these plants were counted at various times, as shown in Table V. The results, as shown in Figure 1, indicate a distinct preference for Latham and King.

TABLE V

Population of *A. rubi* on Three Varieties Grown in the Same Container

Date, 1928	Container No.	Herbert		King		Latham	
		Adults	Nymphs	Adults	Nymphs	Adults	Nymphs
July 30	1	6	..	6	..	6	..
	2	6	..	6	..	6	..
	3	6	..	6	..	6	..
Total		18		18		18	
Aug. 2	1	2	4	2	17	5	45
	2	0	0	10	25	5	24
	3	1	1	3	20	11	76
Total		8		77		166	
" 10	1	0	14	0	69	0	58
	2	0	11	0	63	0	49
	3	0	15	0	42	0	123
Total		40		174		230	
" 15	1	3	24	3	80	2	52
	2	1	19	8	113	4	66
	3	4	22	5	78	4	63
Total		73		287		191	

On August 15 the King and Latham plants (Table V) were removed, leaving only the three plants of Herbert, which were placed in one container. The population of *rubi* decreased at once, as shown in Table VI and Figure 1.

TABLE VI

Decrease in Population of *A. rubi* on Three Plants of Herbert After King and Latham Plants Were Removed

Date, 1928	Herbert		
	Adults	Nymphs	Total
Aug. 15	8	65	73
" 21	4	43	47
" 25	2	36	38
Sept. 2	0	17	17
" 7	0	22	22
" 19	1	14	15

To determine the behavior of *rubi* when each variety is grown in a separate container, 3 plants each of Herbert, Latham, and King were placed under separate street-light globes on July 30, 1928. All aphids had been removed from these plants. Twenty *rubi* nymphs two to

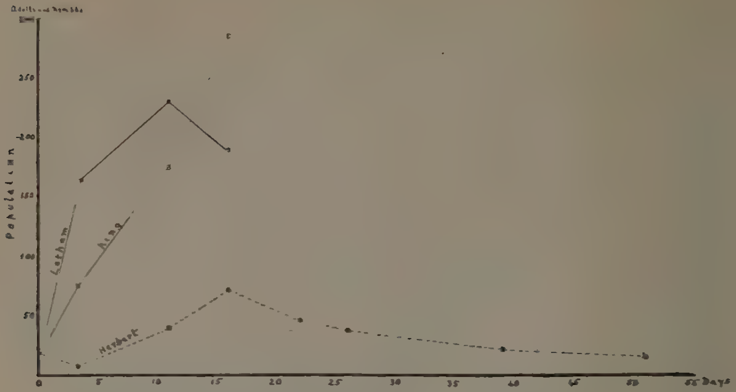

Fig. 1. Population of *A. rubi* on Three Varieties Grown in the Same Container (Table V). Latham and King Removed After 16 Days (Table VI)

three days old were then placed on each plant. A count of the leaflets over one-half inch in length on August 10 showed Herbert 113, King 48, and Latham 48. The *rubi* on these plants were counted at various times, as shown in Table VII. At such times in this and similar experiments all predators or other insect enemies of the aphid were removed. The results, as shown in Figure 2, indicate that *rubi* has great difficulty in maintaining its population on Herbert. There were more leaves on the Herbert than on the two other varieties combined. In spite of this, the population on King and Latham increased far above that on Herbert.

TABLE VII

Population of *A. rubi* on Three Varieties in Separate Containers, Three Plants of Each Variety in Each Container

Date, 1928	Herbert		King		Latham	
	Adults	Nymphs	Adults	Nymphs	Adults	Nymphs
July 30	..	60	..	60	..	60
Aug. 10	..	16	13	117	9	64
" 15	4	39	12	189	21	248
" 21	16	66	plants died		42	386
" 25	5	31	..	..	36	401
Sept. 2	5	29	..	..	11	187
" 7	1	20	..	..	3	131

1928	Adults and Nymphs		
	Herbert	King	Latham
July 30	60	60	60
Aug. 10	16	130	73
" 15	43	201	269
" 21	82	...	428
" 25	36	...	437
Sept. 2	34	...	198
" 7	21	...	134

The data given in Tables VI and VII indicate that *A. rubi* is unable to maintain its population on Herbert under the most favorable conditions—with young tender foliage to feed on and with predators and other insect enemies removed.

TABLE VIII

INCREASE OF *A. rubi* ON LATHAM RASPBERRY AND DECREASE ON HUBERT WHEN CONFINED IN INDIVIDUAL CAGES

Cage	July 30 adults	Aug. 2		Aug. 10		Aug. 15	
		Adults	Nymphs	Adults	Nymphs	Adults	Nymphs
Herbert raspberry							
1 to 10	10	0	0	..	..	..	..
11	1	1	2	0	0	..	..
12	1	1	0	leaf dead		..	..
13	1	1	0	0	0	..	..
14	1	1	0	0	0	..	..
15	1	0	1	0	0	..	..
16	1	1	2	0	0	..	..
17	1	1	0	0	0	..	..
18	1	1	0	0	0	..	..
19	1	1	0	0	1	0	0
20	1	1	0	0	0	..	..
Total aphids	20	9	5	0	1	0	0
Latham raspberry							
1	1	1	0	0	0	..	..
2	1	0	0	..	..	..	..
3	1	1	5	0	4	4	8
4	1	1	3	0	0	..	..
5	1	1	0	0	2	0	0
6	1	1	0	0	0	..	..
7	1	1	4	0	8	0	4
8	1	1	1	0	4	1	14
9	1	1	4	0	0	..	..
10	1	1	4	0	3	0	7
11	1	1	5	0	2	leaf dead	
12	1	1	2	0	1	0	0
13	1	0	0	..	..	..	..
14	1	1	0	0	11	0	1
15	1	1	2	0	5	0	2
16	1	1	5	1	19	0	7
17	1	1	0	leaf dead		..	..
18	1	1	0	0	0	..	..
19	1	1	2	0	3	0	4
20	1	1	0	0	1	0	0
Total aphids	20	18	37	1	63	5	47

The population on Latham increased to 4 adults and 53 nymphs by August 21.

SUMMARY OF TABLE VIII

1928	Herbert	Latham
July 30	20 adults	20 adults
Aug. 2	14 adults and nymphs	55 adults and nymphs
" 10	1 nymph	64 adults and nymphs
" 15	0	52 adults and nymphs
" 21	0	57 adults and nymphs

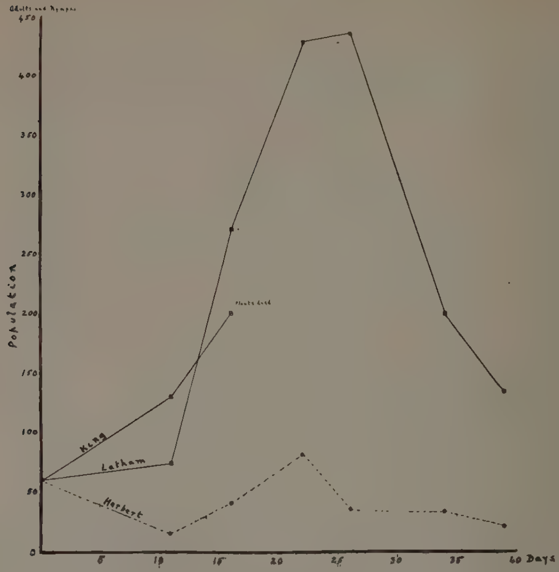

Fig. 2. Population of *A. rubi* on Three Varieties in Separate Containers (Table VII)

Experiments were made under conditions less favorable to the aphid. Each aphid was confined in a glass cage. These cages were obtained through the courtesy of Dr. Walter Carter, who used similar cages in sugar beet investigations. Each cage consists of a glass tube about 2 inches long and less than an inch in diameter. Both ends are open, one end being flared for convenience in covering with cheese-cloth. A metal disk is held by a spring wire against the other end so that the cage may be clamped to a leaf.

On July 30, 1928, twenty cages, each containing one adult *rubi,* were placed on young leaves of Herbert plants so that the aphids could feed on the underside of the leaves. The same number were placed on Latham plants. The aphids in these cages were counted at various times, as given in Table VIII. The aphids placed on Herbert failed to maintain themselves and were all dead after 16 days. Those on Latham increased to about three times their original number in three days and maintained this number for 22 days, when the experiment was discontinued.

To check the data shown in Table VIII a similar experiment was started on September 19, using 10 cages on Herbert and 10 on Latham, with one adult *rubi* in each cage. The data obtained are given in Table IX showing *rubi* unable to maintain its population on Herbert. The Herbert plants used to obtain the data given in Tables V and VI were used in this experiment.

TABLE IX

Decrease of *A. rubi* on Herbert Raspberry When Confined in Individual Cages

1928	Herbert	Latham
Sept. 19	10 adults	10 adults
" 21	5 adults	10 adults
" 24	2 adults	12 adults and nymphs
Oct. 1	1 adult	10 adults and nymphs

Another experiment to check the data shown in Table VIII was started on August 11, 1928, using *rubi* nymphs two to three days old instead of adults. Fifteen cages were placed on Herbert and 15 on Latham, each containing one nymph. The data given in Table X again show that the aphids placed on Herbert were unable to maintain their population. The data given in Tables VIII, IX, and X are shown in Figure 3.

TABLE X

Population of *A. rubi* on Latham and Herbert Raspberry When Confined in Individual Cages

Cage	Aug. 11 nymphs	Aug. 13 nymphs	Aug. 15 nymphs	Aug. 21	
				Adults	Nymphs
Herbert raspberry					
1 to 15	15	1	0	..	..
Total aphids	15	1	0		
Latham raspberry					
1 to 5	5	0	..	..	..
6	1	1	1	0	0
7	1	1	1	0	0
8	1	1	1	1	6
9	1	leaf dead	..	..	..
10	1	1	1	1	5
11	1	1	0	..	..
12	1	1	1	0	0
13	1	1	1	0	0
14	1	1	1	0	6
15	1	1	1	0	0
Aotal aphids	15	9	8	2	17

1928	Herbert	Latham
Aug. 11	15 nymphs	15 nymphs
" 13	1 nymph	9 nymphs
" 15	0 nymphs	8 nymphs
" 21	0 nymphs	19 adults and nymphs

Possible Reasons for Resistance Shown by Herbert

It has been shown that the Herbert variety exhibits a marked resistance to the raspberry aphid, *Amphorophora rubi.* Under field conditions in Minnesota during 1927 and 1928 it seemed unable to exist on the Herbert raspberry, only two being found on 700 leaves selected at random, altho similar counts showed large numbers of this species on several other varieties growing in adjoining rows. Experiments

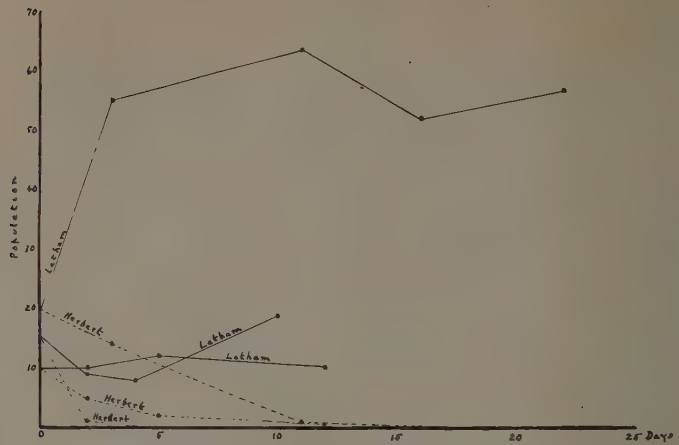

Fig. 3. Population of *A. rubi* on Herbert and Latham When Confined to Individual Cages (Tables VIII, IX, and X)

with potted plants showed that under favorable conditions *rubi* will feed and live on the Herbert variety for several weeks, but is unable to maintain its population. When confined to individual cages the decrease in population was very rapid.

Two possible reasons are suggested to account for the resistance shown by this variety. First, that the leaf of the Herbert is more difficult to penetrate than the leaves of other varieties used for comparison. Horsfall (1923) shows that the objective of the proboscis is always a vascular bundle and the tissue most commonly reached is the phloem, particularly the sieve tubes; also that the route followed by the proboscis indicates a trial and error method of reaching the bundle.

To obtain evidence on the resistance to penetration, adults and nymphs of *rubi* were placed on the under side of leaves of Herbert and Latham. A careful study was made of the time required to assume what appeared to be a normal feeding position with the proboscis fully inserted. No difference in the average time could be noted, the proboscis being inserted with apparent ease on both varieties. At the same time several *rubi* were observed feeding on the upper surface of Herbert leaves. As the cuticle invariably is much thicker on the upper surface, this indicates that thickness of cuticle is not a limiting factor.

Second, a difference in the food material is suggested to account for the resistance shown by the Herbert variety. It is possible that the food materials obtained from Herbert are less compatible to *rubi* than those from the other varieties used for comparison.

APHIDS RECORDED ON RUBUS ARRANGED UNDER THEIR HOST PLANT SPECIES

In compiling this food plant list the writer has endeavored to include all species of Rubus that are definitely recorded in the literature of North America and Europe as host plants of aphids. Every effort has been made to apply the correct botanical name for each host plant. In some instances there is much confusion in published records concerning the host species. Citations to the literature from which these data were obtained are given under the species list of aphids on pages 4 to 11. Several species mentioned in these pages are not included in this list as the data give reasonable assurance that these aphids do not live normally on *Rubus sp.*

Three distinct groups of cultivated forms of the genus Rubus are recognized—the raspberries, the blackberries, and the dewberries. Horticultural varieties of the raspberry grown in North America for their fruit are derived principally from three species, the common red raspberry, *R. strigosus* Michx.; the common black raspberry, *R. occidentalis* Linn.; and the European raspberry, *R. idaeus* Linn.; including hybrids of these species. Three other species are grown to a relatively slight extent—the wineberry, *R. phoenicolasius* Maxim.; the strawberry raspberry, *R. illecebrosus* Focke; and the yellow Himalayan raspberry, *R. ellipticus* Smith. The first two are the only species native to North America, altho in places other species have escaped from cultivation and become established. The blackberries and dewberries under cultivation are derived from a comparatively large number of species of Rubus and their hybrids. These fruits are not generally cultivated except in North America, and the horticultural varieties commonly grown are derived from American species.

Raspberries

R. idaeus Linn. European red raspberry
  Amphorophora rubi (Kalt.) Recorded in Europe
  Aphis idaei Van der Goot. Europe
  Macrosiphum poae (Macchiati). Europe
  Macrosiphum rubiellum Theobald. Europe
  Macrosiphum rubifolium Theobald. Europe
R. occidentalis Linn. American black raspberry, Thimbleberry
  Amphorophora rubi (Kalt.). North America
  Amphorophora rubicola (Oestlund). North America
  Amphorophora sensoriata Mason. North America
  Aphis rubicola Oestlund. North America
  Cerosipha rubifolii (Thomas). North America
  Pemphigus rubi Thomas? North America

R. parviflorus Nutt. Salmonberry, Thimbleberry (syn. *R. nutkanus* Moc.)
    Amphorophora davidsoni Mason. North America
    Amphorophora rubi (Kalt.). North America
    Amphorophora rubicola (Oestlund). North America
R. saxatilis Linn. Dwarf red raspberry
    Amphorophora rubi (Kalt.). Europe
R. strigosus Michx.[8] Common (American) red raspberry
    Amphorophora rubi (Kalt.). North America
    Amphorophora rubicola (Oestlund). North America
    Amphorophora sensoriata Mason. North America
    Aphis rubicola Oestlund. North America
Red Raspberry, American cultivated
    Amphorophora rubi (Kalt.). North America
    Amphorophora rubicola (Oestlund). North America
    Amphorophora sensoriata Mason. North America
    Aphis rubicola Oestlund. North America
Raspberry (*Rubus sp.*) No other host data available.
    Amphorophora reticulata Mason. North America
Salmonberry. (Probably *R. spectabilis* Pursh or *R. parviflorus* Nutt.)
    Amphorophora maxim Mason. North America

Blackberries

On account of the large number of species and hybrids involved in both the wild and cultivated blackberry, it is not possible to name the probable species when specific names are not stated by the collector. Hedrick (1925) describes 29 species of blackberry native to North America, including 4 species naturalized from Europe. He mentions 8 species and their hybrids from which our horticultural varieties are derived.

R. fruticosus Linn. European blackberry
    Amphorophora rubi (Kalt.). Europe
    Macrosiphum rubiellum Theobald. Europe
    Macrosiphum rubifolium Theobald. Europe
Blackberry (*Rubus sp.*) No other host data available.
    Aphis rubicola Oestlund. North America
Blackberry, American native
    Amphorophora rubi (Kalt.). North America
    Cerosipha rubifolii (Thomas). North America
Blackberry, American cultivated
    Amphorophora rubi (Kalt.). North America
    Cerosipha rubifolii (Thomas). North America

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[8] Hedrick (1925) considers *R. strigosus* a sub-species of *R. idaeus*. Rosendahl and Butters (1927) state that these are two distinct species.

Dewberries

Hedrick (1925) describes 18 species of dewberry native to North America including one species naturalized from Europe, and mentions 6 species and their hybrids from which are derived the horticultural varieties cultivated for their fruit. Most of the northern dewberries are derived from *R. flagillaris* including the variety Lucretia.

R. caesius Linn. European dewberry
  Amphorophora rubi (Kalt.) Europe
R. flagillaris Willd. Northern dewberry (syn. *R. procumbens* Muhl.)
  Amphorophora rubi (Kalt.). North America
R. Loganbaccus Bailey. Loganberry
  Amphorophora rubi (Kalt.). North America
  Aphis rubicola Oestlund. North America
R. villosus (Species uncertain, several synonyms)
  Macrosiphum ambrosiae (Thomas)? North America

Rubus Sp.

Rubus. sp. No other host data available.
  Aphis mordwilkiana Dobr. Europe
Rubus corylifolius
  Amphorophora rubi (Kalt.). Europe
Rubus discolor
  Amphorophora rubi (Kalt.). Europe

SUMMARY

A brief account is given of the aphids found on the bramble fruits in North America and in Europe including their synonomy and host plants. Five species are found widely distributed in North America. Five additional species are recorded, two of which are questionable records. Six species are found in Europe. Six other species are recorded in Europe under circumstances indicating that the bramble fruits are not their normal host. Only one species is common to North America and Europe.

Notes are given on the biology and morphology of three species of aphids common in Minnesota, *Amphorophora rubi* (Kaltenbach), *Amphorophora rubicola* (Oestlund), and *Aphis rubicola* Oestlund. Eggs of *A. rubi* and *Aphis rubicola* have been collected, and these two species have been followed on the raspberry throughout the year.

A study was made of the distribution and movement of wingless forms of *A. rubi.* It was found that this aphid may be carried on the clothes of persons from one raspberry planting to another and that

distribution occurs within a planting when the foliage is disturbed by cultural operations and by digging of plants. It is shown that this aphid does not remain on leaves that have wilted.

The Herbert raspberry exhibited a very marked resistance to *A. rubi*. Under favorable conditions, with its insect enemies removed, *rubi* will feed and live on the Herbert variety for several weeks but is unable to maintain its population. The population on check plants of other varieties invariably increased, often at a rapid rate.

Under field conditions, *rubi* seemed unable to exist on Herbert in the plantings where observations were made for two years, altho many were found on other varieties growing in adjoining rows. The proboscis of this aphid is inserted with apparent ease in the leaves of the Herbert variety, indicating that thickness of cuticle is not a limiting factor.

A list is compiled of the aphids recorded on Rubus in North America and in Europe, arranged under their host plant species.

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Daily Growth of the Oat Kernel and Effect on Germination of Immaturity and Controlled Low Temperatures

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CONTENTS

Page

Introduction 3

Acknowledgments 4

Review of the literature 4

Progressive development of the oat kernel 8
  Materials and methods 9
  Detailed study of pollination in florets of the same panicle 12
  Changes in physical measurements 14
  Changes within the kernels 19
  Relationship between external and internal characters 24
  Application of daily growth study to farm practices 26

Effect on germination of immaturity and controlled low temperatures 27
  Materials and methods 27
    Technic of exposure to controlled low temperatures 28
    Germination tests 30
  Laboratory germination of samples exposed to controlled low temperatures 31
  Field germination of samples exposed to controlled low temperatures 34
  Comparison of fifteen-day average germinations 36
  Comparison of laboratory and field germinations 37
  Correlation between dry matter and germination 38

Effect of exposure to controlled low temperatures on the green leaves and stems of immature oat plants 39

Summary and conclusions 40

Literature cited 41

ILLUSTRATIONS

Page

Fig. 1. Panicles of Gopher oats 9

2. Relative stages of development in the same panicle at three days 13

3. Relative stages of development in the same panicle at nine days 15

4. Appearance of kernels during development 17

5. Changes in length, width, and thickness 18

6. Changes in green and dry weights 21

7. Changes in nitrogen and ash, by weight 22

8. Changes in nitrogen and ash, by percentage 23

9. Comparison of mean germinations in laboratory and field 32

DAILY GROWTH OF THE OAT KERNEL AND EFFECT ON GERMINATION OF IMMATURITY AND CONTROLLED LOW TEMPERATURES[1]

ERNEST GORDON BOOTH

INTRODUCTION

The effect of temperatures of 32°F. (0°C.) or lower on the germination of oats before the crop has matured, is a question of economic importance with the northward expansion of the oat-growing area. Regions having climatic conditions favorable to the development of the oat plant frequently have early fall frosts. Even in less northerly latitudes, the oat crop, when of necessity sown late, is occasionally harvested in an immature condition after an early frost. Each year the seed laboratories test many samples of oats that are unfit for seed because of low viability. The cause of poor germination is uncertain, but it is frequently attributed to frost injury.

In a study of the effect of freezing temperatures on germination three conditioning factors are to be considered, as follows: The actual temperatures, the duration of the exposure to low temperatures, and the stage of kernel development. Without doubt each of these factors has a contributing or counterbalancing effect. Immaturity may be as important as temperatures at or below 32°F. (0°C.) in lowering the average germination.

It is also desirable to know the effect of low temperatures on different varieties of oats throughout the period of kernel development or any part of it.

In planning this investigation, consideration was given to each of these problems. The daily changes in the development of the oat kernel[2] were observed and an effort was made to determine whether any critical period existed when the injury from exposure to low temperatures might be severe. Oat kernels in different stages of development were exposed to controlled temperatures both above and below 32° F. (0°C.).

A study of the daily growth of the oat kernel should also throw some light upon the question of when to cut the crop to obtain maximum yield and quality. These factors are closely related to the time of harvesting and there is need for exact knowledge of the relationship existing between external and internal evidences of maturity.

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[1] A thesis submitted to the faculty of the Graduate School of the University of Minnesota in partial fulfillment of the requirements for the degree of Doctor of Philosophy. Degree granted 1928.

[2] The term "kernel" is used to indicate the fertilized pistil during its development.

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REVIEW OF THE LITERATURE

The development of wheat and barley kernels has been studied by European investigators, but these studies were prompted by a desire to learn more about the development of protein and starch in the caryopsis. Besides working with a different object in view, the climatic conditions under which the work was accomplished were very different, the growing season being much longer and the precipitation greater. As a result, the work of early European investigators apparently has little bearing upon the present problem.

Johannsen (1884) studied the development of the barley kernel at three-day intervals. His work included a careful chemical and cytological study of development from blossoming time to maturity. Starch grains appeared very early in the development of the kernel.

Schjerning (1906, 1914) made a detailed study of the protein at different stages of maturity in several varieties of barley. He concluded that environment was more effective than variety in determining the total nitrogen content. In his studies, the growing period was divided into two stages—developmental and ripening. To quote his conclusions is illustrative. "At the close of the developmental period the barley grain has reached its maximum volume, at the end of the ripening period its highest amount of dry matter. At the moment when the grain has reached the stage of full maturity we have (allowance being made for analytical errors) reached the maximum values for dry matter, ash, acid, and total insoluble nitrogen." Over-ripening caused loss of these materials. "Yellow ripeness" was his measure of maturity.

Brenchley (1912) and Brenchley and Hall (1909) studied the development of barley and wheat at three-day intervals. In barley, nitrogen and ash increased steadily until ripening began. Nitrogen then increased and ash decreased. The dry weight increased uniformly during the developmental stage. During this period, the water content of the kernels in both crops was also similar. The nitrogen content varied slightly in different stages. Brenchley concluded that the progressive changes in the two grains are parallel, tho varying in detail. The prolonged ripening period of barley, during which maturation changes occurred, was held to be the chief difference. A comparison of the changes in the cell in both wheat and barley showed the course of the phenomena to be exactly similar. The cells in the flanks showed the first infiltration of starch and disorganization of the protoplasm. The sub-aleurone and furrow cells showed the last changes.

Thatcher (1913, 1915) harvested spikes of three varieties of spring wheat at three-day intervals. The spikes were tagged when the largest proportion of them showed anthers protruding from the central spikelets. The percentage of protein in the dry matter decreased slightly until the milk stage, then increased to maturity. The mature samples contained more protein than the very immature ones. The actual quantity of each material except sugars increased with each period of harvest. The carbohydrate-protein ratio diminished with the successive harvests.

Kedzie (1880, 1881, 1893), as early as 1879, working in Michigan, studied the daily development of the wheat kernel. Measurable growth occurred in each twenty-four hour period. Just after flowering, the ash content was 4.72 per cent of the dry matter. When the first starch grains appeared, on the seventh day, the percentage of ash was reduced to 3.42, and on the twenty-seventh day, when the kernels were becoming hard and flinty, it was 2.13. The crude protein content for the same days was 36.22, 22.76, and 11.69 per cent, respectively.

The daily increment of dry matter was rapid and, in effect, a straight line increase until about the twelfth day. From this period until near maturity the increase in dry matter was slow. A loss was noticeable after the kernels were hard.

Harlan (1920) studied the kernel development of Hannchen barley. He made daily physical measurements at twelve-hour intervals. Measurable growth occurred during these periods. Development was very rapid just after pollination and length growth was completed by the seventh day. The increase in width then became rapid for a short time. The kernel continued to increase in thickness steadily until near maturity. The increase in dry matter and the decrease in the percentage of water were uniform until the kernels were ripe. The ash content varied from 8.96 per cent of the dry matter during the first few days to less than 2 per cent when the grain was mature. There was a variation in nitrogen from 4.45 per cent of the dry matter to about 2 per cent in the same direction as the ash.

The same author (1923) found that the laying down of dry matter ceased when the average moisture content for all the kernels of a spike was about 42 per cent. There was also a decrease in physical measurements toward the end of the maturation period.

Dillman (1928) studied the daily development of flax seeds. Daily physical measurements were recorded and samples were analyzed to determine when the oil was laid down. Growth was rapid and uniform up to the thirteenth day, when maximum size was attained. All three dimensions increased during this time. During the ripening period there was a decrease in size. The green weight also approached its maximum in the same period but, unlike the cereals, did not begin to decrease until after the twenty-second day. The increase in dry weight was slow during the first few days, then slightly more rapid and uniform until the end of the developmental period. The moisture percentage started at 85 and did not begin to decrease until after the eighth day. The decline was then uniform.

Oil first appeared between the fourth and sixth days. The quantity increased rapidly until the eighteenth day, then slowly until the thirtieth day. The amount of oil increased after the percentage was stationary.

The developmental period extended over about thirty days, but the flax was not considered ripe until the thirty-ninth or fortieth day after pollination.

Controlled experiments to determine the effect of temperatures of 32°F. (0°C.) or lower upon germination have been difficult to perform until recent years. The lack of suitable laboratory equipment and the uncertainty of climatic conditions favoring such experiments have limited the number of attempts to study the effect of frost injury on germination. Fryer (1919) planted oats at weekly intervals in the spring to obtain samples in different stages of maturity at the time frosts occurred in the fall. He found that 2.3 degrees, 29.7°F. (−1.3°C.) of frost (presumably Fahrenheit degrees) did not reduce the vitality of samples ranging in development from very early milk to dough. Similarly, 4.6 degrees, 27.4°F. (−2.6°C.), did not injure samples in the milk stage to the mealy dry stage. Samples in the dough to the mealy dry stage were not injured by 5 to 8 degrees, 27° to 24°F. (−2.7° to −4.4°C.), but those in milk to dough stages were considered injured. The twelve-day germination of the latter group was reported as 76 to 92 per cent before freezing and three days later after two frosts, one of 5 degrees, 27°F. (−2.7°C.) and the other of 8 degrees, 24°F. (−4.4°C.), the germination ranged from 45 to 61 per cent. The duration of the temperatures of 32°F. or below, the dry matter content, and the number of samples averaged to obtain each germination report were not given. Registered Banner oats were used in the experiment. In most cases the very immature samples had a slightly lower germination than the more mature samples. This was apparently not consistent enough, or of a sufficient degree, to be commented upon by the author. The same author (1921) at a later time planted oats at different periods in the spring and succeeded in getting two samples in the late dough stage frozen at different temperatures. One sample was subjected to a temperature of 23.5° F. (—4.8° C.) and the other to the same temperature and also to temperatures of 19° F. (—7.2° C.) and 30° F. (—1.1° C.) on succeeding nights. The duration of the periods at these temperatures was not given or any of the details regarding the germination tests. The final germination of these samples was reported as follows: check, not frosted, 97 per cent; 23.5° F. (—4.8° C.), 81 per cent; 23.5° F. (—4.7° C.), 19° F. (—7.2° C.) and 30° F. (—1.1° C.), 61 per cent. He found that freezing tended to fix the greenish color, particularly at the germ end, if the oats were very immature. Presumably this refers to the remaining floral parts, including the lemma and palea. Brittleness was increased and the interior of the endosperm was frequently darkened as well as the strand of tissue that traverses the bottom of the groove.

Johnson and Whitcomb (1927) reported that immature wheat kernels were injured by temperatures of 32°F. (0°C.) or below. The effect of immaturity was apparently not included in the study. Both field frosts and a controlled temperature of 27° F. (—2.7° C.) for twenty-four hours were included in the tests. With these temperatures, there was enough injury in a few samples to reduce the germination materially. They found germination of four frosted samples to be decidedly lower in the field than in the laboratory.

Kiesselbach and Ratcliff (1920) found that freezing immature or moist corn discolored the embryo. When the moisture content was above normal, the germination was injured in proportion to the percentage of moisture and the duration of the frost.

In recent years there has been a tendency to question whether the laboratory test is an adequate gauge of the field germination. Whitcomb (1924) found that over a four-year period the field germination of 164 samples of oats averaged 15 per cent less than the most favorable laboratory germination. The average germination of 641 samples of wheat was 20 per cent lower in the field. Ten kinds of agricultural seeds were included in this test and 1,298 samples were germinated during the four years, in both the laboratory and the field. The average germination was 24 per cent lower in the field than in the laboratory. It is interesting to note that in three out of four years field peas germinated at a higher rate in the field.

Wright (1921) found that oats germinating between 70 and 100 per cent in the laboratory showed an average of 10 per cent less in the field. When the laboratory germination was below 65 per cent, the field germination averaged 21 per cent lower. Other field-crop seeds showed a similar tendency. The difference between laboratory and field germination tests was more pronounced with the smaller seeds.

Several investigators have noticed the lack of vigor in young plants produced from seeds that were harvested before they were normally ripe. Crozier (1895) germinated wheat harvested in the milk, dough, yellow ripe, and dead ripe stages. The seeds harvested in the milk stage germinated the most rapidly. These seedlings were feeble and pale and were soon passed in growth by those from more mature seeds. Seeds harvested in the yellow ripe stage germinated most vigorously. Harlan (1922, 1926) found that barley kernels harvested five and six days after pollination would germinate. The seedlings were much less vigorous and, when transplanted, produced plants that were less robust than those from mature kernels. Methods of drying the immature seeds materially affected the development of both the endosperm and the embryo. When the kernels remained in the spike and it was not allowed to become dry, the endosperm and the embryo continued to develop for at least eight days. There was less development when the kernels were air-dried in the lemma and palea, whether they remained in the head or were detached. The embryos of immature kernels from which the lemma and palea had been removed did not develop further unless the kernels were kept moist.

Alberts (1926) obtained weak plants on germinating corn harvested in an early stage of development. Seeds gathered in the milk stage germinated poorly and showed weak sprouts. When harvested in the late milk stage there was a decided improvement, but the germination was still unsatisfactory and the seedlings were weak. Seeds harvested in the dough stage germinated satisfactorily and produced strong seedlings.

Kiesselbach and Ratcliff (1920) found that delaying the harvesting of corn until the kernels reached the late dough stage increased the percentage of germination.

PROGRESSIVE DEVELOPMENT OF THE OAT KERNEL

It seemed logical in attacking the problem in hand to study the development of the oat kernel first. With this information in mind, it should be easier to interpret the results obtained in later studies.

Materials and Methods

Gopher oats, Minnesota No. 674, developed and grown at University Farm, St. Paul, was used for the study. A typical panicle of this early, high yielding variety of white oats is shown on the left in Figure 1.

The seed for the experiment was planted with the grain drill on one of the regular experimental plots on April 20, 1926. The soil is classified as Hempstead silt loam and consists of black loam underlaid with a small amount of clay which merges into sand and gravel at 8 to 10 feet.

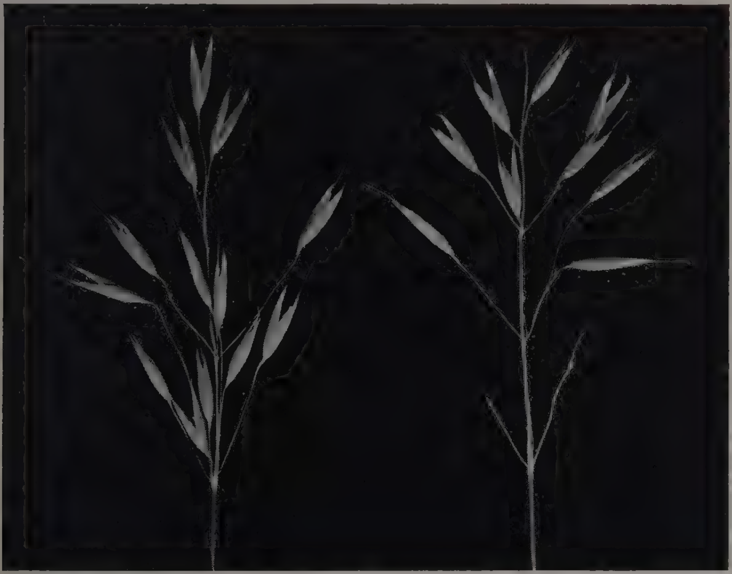

Fig. 1. Panicles of Gopher Oats
Left. Typical Panicle
Right. Panicle of Gopher Oats with the Spikelets Discarded in the Daily Studies Removed

The spring and early summer were unusually dry, with practically no rainfall during April, May, and the first ten days of June. A comparison of the precipitation and temperature during this period with past averages is included in Table I. While the precipitation was much less, the mean temperature did not vary greatly from the long-time average for the respective months.

As a result of the lack of moisture during early growth, the oats headed out with shorter straw than usual, the height being 24 inches as compared to the usual length of about 30 inches. The yield was 34.1 bushels as compared to the seven-year average of 58.5 bushels per acre. Timely rains in June caused normal growth and filling of the kernels from before heading until harvest. Despite adverse conditions during early growth, the stand was fairly uniform at heading time.

TABLE I

DAILY WEATHER OBSERVATIONS DURING KERNEL DEVELOPMENT, JUNE 29 TO JULY 24, AND MONTHLY AVERAGES, AT ST. PAUL, 1926

Date	Precipitation, in.	Maximum temperature, ° F.	a.m.	p.m.
June 29	...	85	Cool and cloudy	Clear
30	...	80	Cool	Cool
July 1	0.56	73	Rain, clouds	Cloudy, sultry
2	T	79	Cloudy, cool	Cloudy, sultry
3	...	82	Clear, cool	Clear, warm
4	0.06	79	Cloudy, cool	Cloudy, showers
5	...	82	Clear, warm	Clear, warm
6	...	88	Clear, warm	Clear, hot
7	...	86	Clear, warm	Clear, hot
8	T	90	Cloudy	Clear, sultry
9	0.25	78	Cloudy, cool	Cloudy, cool
10	...	73	Clear, cold	Cloudy, cool
11	T	80	Clear, cool	Cloudy, cool
12	...	68	Clear, cool	Clear, cool
13	...	73	Clear, cool	Clear, cool
14	...	77	Clear, warm	Clear, cool
15	T	85	Cool	Hot, high wind
16	...	98	Clear, warm	Clear, hot, breezy
17	...	86	Clear, warm	Clear, warm
18	T	94	Clear, cool	Clear, hot, breezy
19	0.03	89	Cloudy, sultry	Clear, hot
20	0.47	99	Cloudy, sultry	Clear, sultry
21	0.41	73	Cloudy, cool	Clear, cool
22	0.02	79	Clear, warm	Cloudy, cool
23	0.15	73	Cloudy, cool	....
24	0.26	69	Cloudy, warm	....

	Precipitation				Maximum temperature, ° F.				
	April	May	June	July	April	May	June	July	
Total	0.53	1.37	3.65	2.92	43.8	61.4	63.7	71	Mean
Normal	2.33	3.62	4.41	3.40	45.6	56.4	67.1	72.	Normal

The first heading occurred on June 27 and apical spikelets were visible on about one per cent of the panicles on June 29, when the first tagging was done. By previous observation it was determined that the florets of the apical spikelets in different panicles were at a uniform stage of development when first appearing out of the sheath. Accordingly, this was taken as a basic stage in development and several hundred such panicles were tagged on June 29. Panicles in the same stage of development were tagged on June 30, July 2 and 3. The tagging was done with short lengths of colored yarn to distinguish between the plants that represented twenty-four-hour periods in development. More than eight hundred panicles were tagged for the study.

Observations on oats sown at an earlier date in the same year indicated that there was a considerable lapse of time between the pollination of the upper and lower spikelets in the panicle. To obtain a group of kernels that were in a similar stage of development in the same panicle it was necessary to remove the apical spikelet and all the spikelets of the lower whorl. In addition, the spikelet with the shortest pedicel in the middle whorl was removed, as shown in Figure 1. The secondary floret in each spikelet was later in fertilizing than the primary floret and a further distinction was made by using only primary florets.

As soon as general pollination of the florets used in this study had taken place, samples were gathered from different parts of the plot each morning at about seven o'clock. The tagged plants were pulled with the roots attached and were wrapped in a damp cloth before they were removed from the field. The first operation in the laboratory was to remove the overmature and undermature kernels, as illustrated on the right in Figure 1 and previously discussed.

The sample gathered each day was divided into two portions. One part was used to determine the physical measurements, dry matter, and ash. This sample consisted of twenty kernels selected from three or four panicles. To minimize drying after removing the flowering glumes, with a consequent change in size, the work was done rapidly. In each case groups of five kernels were used. In the regular procedure the hulls from one group were quickly removed and the kernels placed on a glass slide. By drawing the glass under the lens of a high-power binocular fitted with a measuring eye-piece, the length and width could be recorded at once. The kernels were then placed on edge with a dissecting needle to determine the thickness. Measuring the four groups required about twenty minutes, and as soon as the measuring of each group was completed, the kernels were placed in a covered weighing bottle. The green weight of the twenty kernels was next determined, and immediately afterward the sample was placed in a drying oven for twenty-four hours at 204.8°F. (96°C.). After weighing and checking the dry weight, the same twenty kernels were used in determining the ash content.

The other part of the sample gathered each day was set aside to be used in determining the nitrogen content. To obtain a large enough sample for chemical analysis, it was necessary to use six panicles. The spikelets were stripped from these panicles and dried for one hour at 204.8°F. (96°C.). The daily samples were then placed in paper envelopes and stored in a metal box until analyzed.

Daily weather observations were made from June 29 to July 24. During this period, the precipitation was slightly below normal. There were several heavy rains and periods of intense heat. Responses to these occurrences could be readily noted in the daily studies.

Table I indicates that during July, when daily samples were being gathered, the total precipitation was 2.92 inches. The average July precipitation for several years is 3.40 inches. The mean temperature for the month was 71.8°F. (22.1°C.) as compared to a past average of 72.1°F. (22.3°C.). These records indicate that the weather during July was nearly representative.

Confusion exists in the literature as to the meaning of such terms as "developmental period," "maturity," and "ripe." In this paper, the first term is used to designate the period during which rapid growth changes are taking place in the kernel. Following the developmental stage, there is a period of ripening. The term "mature" is used to indicate the time at which harvesting would ordinarily take place. Such expressions as "ripe" and "yellow ripe" are used with the same meaning as the word "mature" and mean the accepted time of harvesting as previously expressed. In the discussion that follows, the term "width" has been used to express the lateral measurement of the kernel; the word "thickness," to designate the dorso-ventral measurement. There is also frequent reference to pollination in the floret. When the anther sacs become ripe they break open and deposit pollen on the stigmatic surfaces. The time during which the pollen is deposited is referred to as the period of pollination.

Detailed Study of Pollination in Florets of the Same Panicle

The difference in time of pollination within the panicle observed while examining oats seeded at an earlier date prompted a more complete study of pollination by using some of the tagged plants. Observations on the panicles tagged June 29 showed that during the first day from three to five of the spikelets emerged from the boot. The stamens, style branches, and ovaries in all these spikelets were very immature, being greatly compressed and firm. The next day the panicles were about two-thirds emerged from the boot and the apical primary floret had pollinated. A few withered anthers were also visible, indicating that the lemma and palea had opened slightly. On July 1 the panicles were just clear of the sheath. The weather turned cool at this time and apparently little or no further change occurred until July 3, when the majority of the florets shown in the panicle on the right in Figure 1 pollinated.

Pollination in the florets could be detected by the behavior of the style branches. Within a few hours after the pollen was deposited upon the stigmatic surfaces, the style branches curved inward at the apex. The stigmatic surfaces were, therefore, soon pressed firmly together, as indicated in Figure 2. For convenience in identification, those in the vertical series in Figure 2 have been numbered 1 to 5, and those in the horizontal series 6 to 11, inclusive. At the intersec-

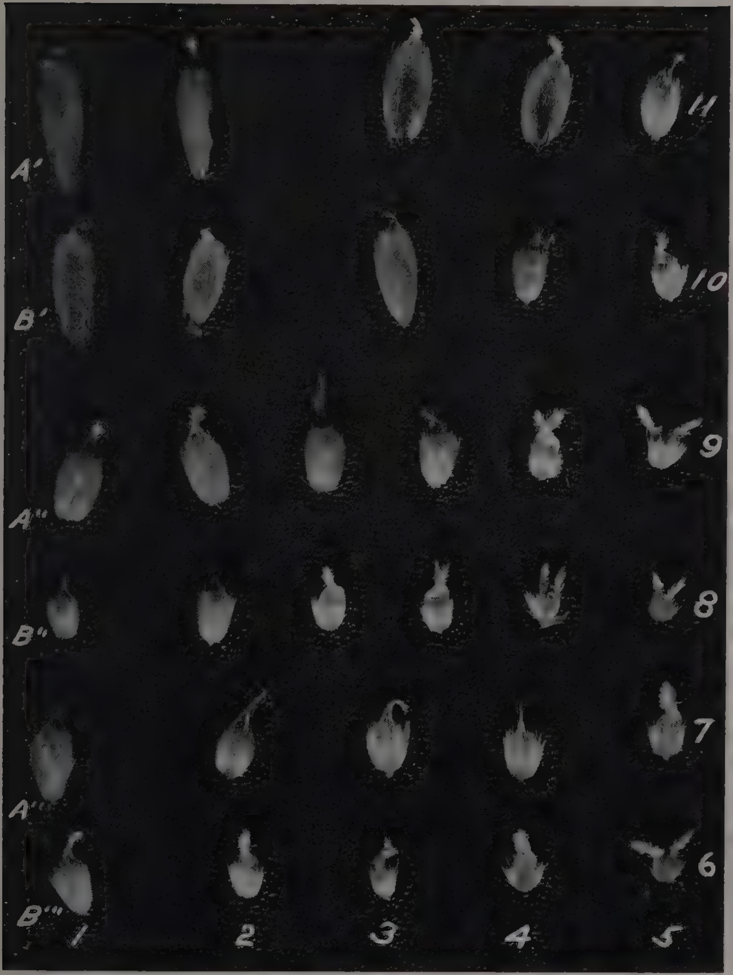

Fig. 2. Relative Stages of Development in the Same Panicle

The photograph was taken three days after general pollination of florets in the upper and middle whorls. The kernels from a complete panicle, as shown on the left in Figure 1, are included in this illustration. The series marked A are primary kernels and those marked B are the secondary kernels from the same spikelet. Starting at the upper left-hand corner and reading from left to right, the series A′, A″, A‴ represent the order of arrangement of kernels in the panicle from the apex downward.

tion point of vertical series 4 and horizontal series 8, two styles are just converging. The pistil immediately above it, 4-9, was pollinated some hours earlier, and the stigmatic surfaces are pressed past each other; 5-9 is still unpollinated. About twenty-four hours after pollination the style branches withered slightly, as shown in 5-10, and were dry and brown at forty-eight hours, as shown in 3-7 and 4-7. These photographs show clearly that pollination took place in the secondary florets twenty-four to seventy-two hours later than in the primary florets. This can be observed by referring to specific primary florets and the secondary florets of the same spikelets. In Figure 2 kernel 5-10 is the secondary and 5-11 the primary kernel in the same spikelet with 5-10 about forty-eight hours behind 5-11. Kernel 2-6 is also about forty-eight hours behind its primary kernel 2-7.

The first pollination in the apical spikelets occurred on June 30. Pollination of the florets in the lower whorl began on July 4 and the process continued progressively downward until July 8, when it was complete. Pollination, therefore, extended over a period of eight days. Harlan (1926) observed that barley florets located in the middle of the spike were the first to pollinate. Later pollination occurred in both directions from the middle.

Figure 2 illustrates the range of maturity in a representative panicle three days after pollination of the florets giving rise to the kernels used in this study, and in Figure 3 is brought out the range of maturity of the kernels in another representative panicle at nine days. In Figure 2 kernel 1-11, which was produced by the apical primary floret, is nearly full length; the stigmatic surfaces of 5-6, a secondary floret, in the lower whorl, have not been pollinated. The relative uniformity of the kernels used in this study during their early development is also illustrated in Figures 2 and 3. In Figure 2 kernels 2-11, 3-11, 4-11, 5-11, 1-9, and 2-9 represent the group studied. In Figure 3, the kernels included in this group are numbered 2-11, 3-11, 4-11, 1-9, and 2-9. Altho there is considerable difference in length, the withered style branches attached to the kernels mentioned, particularly those in Figure 2, indicate that the florets were pollinated at approximately the same time. The uneven development in length was not very noticeable after the first few days.

Changes in Physical Measurements

The length, width, and thickness of the twenty kernels from which the hulls had been removed were each averaged and are reported in Table II.

Length.—The length measurements given in Table II show the daily range in twenty kernels. These differences are considerable and may be due to time of pollination or growth rate. After the early rapid growth period, there was a tendency to smooth out these irregularities.

During the first six days there was a rapid increase in length, the kernels developing 82.3 per cent of the maximum length reached on the fifteenth day. The mean length increased slowly from the sixth to the fifteenth day, but many of the kernels had reached full length by the tenth and eleventh days.

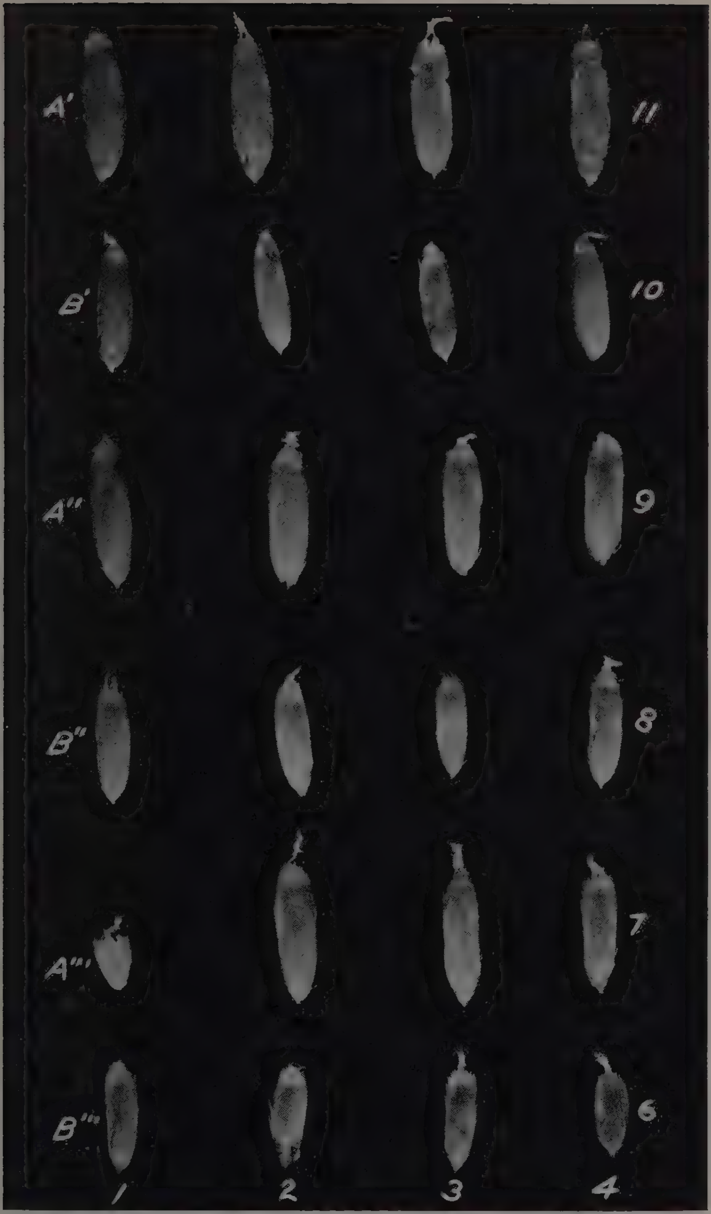

Fig. 3. Relative Stages of Development in the Same Panicle

The photograph was taken nine days after general pollination of the kernels in the upper and middle whorls. The kernels from a complete panicle, as shown on the left in Figure 1, are included in this illustration. The series marked A are from primary florets and those marked B are the secondary florets from the same spikelet. Starting at the upper left-hand corner and reading from left to right, the series A′, A″, A‴ represent the order of arrangement of kernels in the panicle from the apex downward.

TABLE II

Daily Measurements of Length, Width, and Thickness of Gopher Oat Kernels

Date	Days after pollination	Determinations on 20 primary kernels with the hulls removed									Stage in development
		Length			Width			Thickness			
		Average	Range	Per cent of maximum	Average	Range	Per cent of maximum	Average	Range	Per cent of maximum	
		mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	
July 4	1	1.89	1.3- 2.6	20.6	2.03	1.5-2.2	69.5	1.62	1.3-2.0	64.5	
5	2	2.60	1.5- 4.1	28.3	2.17	1.9-2.6	74.3	1.83	1.6-2.0	73.3	
6	3	4.47	2.8- 7.5	48.7	2.51	2.1-2.7	85.9	1.92	1.7-2.2	76.4	
7	4	5.80	3.9- 8.3	63.2	2.60	2.3-2.9	89.0	2.06	1.8-2.3	82.0	
8	5	6.25	3.3- 8.7	68.1	2.66	2.3-2.8	91.0	1.99	1.8-2.1	79.2	
9	6	7.55	5.8- 9.0	82.3	2.66	2.4-3.0	91.0	2.10	1.9-2.3	83.6	Early milk
10	7	7.64	6.8- 8.8	83.3	2.64	2.5-2.9	90.4	2.18	1.9-2.5	86.8	
11	8	8.24	7.8- 9.1	89.8	2.73	2.5-3.0	93.4	2.26	2.1-2.4	90.0	First yellow color
12	9	8.47	7.8- 9.1	92.3	2.81	2.6-3.0	96.2	2.38	2.3-2.6	94.8	Late milk
13	10	8.64	8.0- 9.7	94.2	2.85	2.6-3.0	97.6	2.42	2.2-2.7	96.4	General yellow color
14	11	8.84	8.3- 9.4	96.4	2.91	2.6-3.1	99.6	2.46	2.2-2.7	98.0	Early dough
15	12	8.81	8.0- 9.5	96.0	2.92	2.7-3.1	100.0	2.45	2.3-2.7	97.6	
16	13	9.01	8.0- 9.6	98.2	2.87	2.6-3.1	98.2	2.51	2.1-2.7	100.0	Dough
17	14	9.06	8.0- 9.8	98.8	2.64	2.1-2.9	90.4	2.31	2.0-2.6	92.0	
18	15	9.17	8.3-10.0	100.0	2.76	2.3-3.2	94.5	2.39	2.0-2.7	95.2	First ripe
19	16	8.86	8.1- 9.5	96.6	2.56	2.1-2.9	87.6	2.24	1.8-2.6	89.2	
20	17	8.79	8.3- 9.3	95.8	2.53	2.2-2.9	86.6	2.16	1.8-2.5	86.0	General ripe
21	18	8.89	8.4- 9.3	96.9	2.31	2.1-2.6	79.1	1.98	1.8-2.2	78.8	
22	19	8.84	8.5- 9.3	96.4	2.43	2.1-2.7	83.2	2.06	2.0-2.2	82.0	
24	20	8.70	8.1- 9.1	94.8	2.25	2.0-2.5	77.0	1.93	1.8-2.2	76.0	
24	21	8.66	8.0- 9.6	94.4	2.26	2.0-2.2	77.3	1.94	1.8-2.1	77.3	

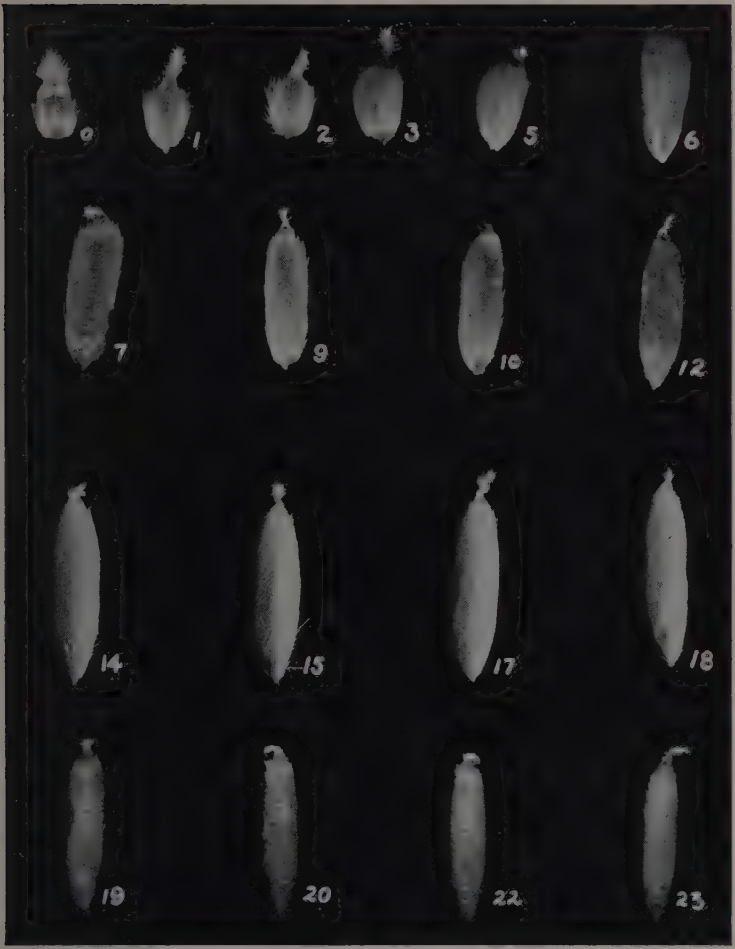

Fig. 4. Appearance of Kernels During Development
The number indicates the days after pollination.

Maximum development in length was reached on the fifteenth day and thereafter there was a tendency to decrease in length as the percentage of dry matter increased and ripening progressed. In the last sample harvested the kernels averaged only 94.4 per cent of the maximum length. The rapid falling away in length between the fifteenth and sixteenth days was due to extreme desiccation caused by three very warm days preceding this date. There was a tendency to reestablish the length after rains, which occurred on three days following the warm weather.

The mean daily increase in length as shown in Table II is presented graphically in Figure 5.

Width and thickness.—In the early stages of development, the germ end of the kernel was partly obscured by a dense growth of fine hairs (Fig. 4, kernels 1, 2, and 3). This did not interfere with measuring the length, but the width and thickness could be measured during the first few days only by including the hairs. After the second or third day this difficulty did not exist, because the growth in length spread the hairs over a greater area, making the surface visible. All measurements were made at the widest point. During early growth, the brush end was somewhat truncate and the widest part was near this end. As the length increased, the brush end tapered and the widest part of the kernel approached the middle.

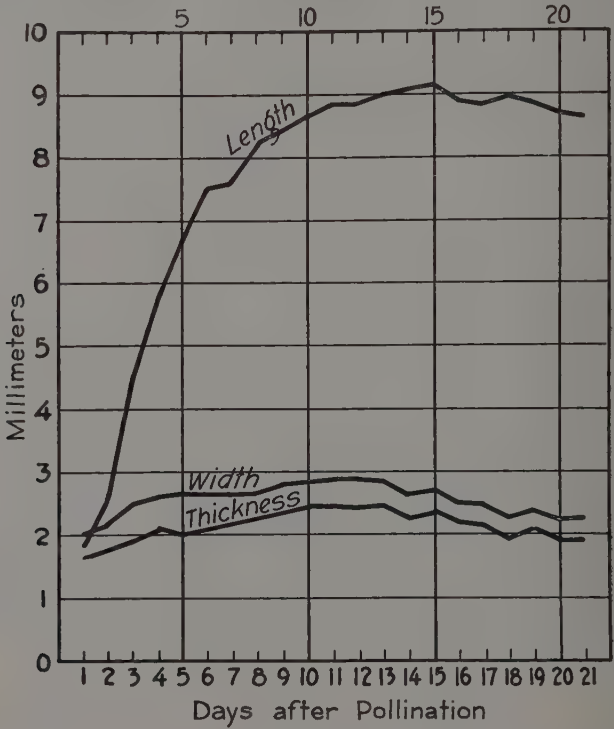

Fig. 5. Daily Growth Change in Length, Width, and Thickness from the Day After Pollination Until Maturity

A study of the development in width shows that there was a rapid increase during the first three days, approximately 86 per cent of the growth in width being completed during this period. The daily means are given in Table II and illustrated graphically in Figure 5.

From the third to the eighth day after pollination, little change in measurement was recorded. Beginning with the eighth day, there was a second period of expansion up to the twelfth day, when maximum width was reached.

The width of a few kernels was noticeably affected by the heat from the thirteenth to the fifteenth day. On the second warm day, desiccation had progressed to the point of drawing in the side walls. The damp weather following the warm period did not re-establish the width of these kernels.

As the caryopses increased in dry matter toward the end of the developmental period, the width decreased. At the time the crop was considered ripe, the width was only 86.6 per cent of the twelfth-day average. With delayed harvesting, there was a further decrease in four days to 77.3 per cent of the maximum.

The figures indicating the mean daily trend in thickness are contained in Table II and graphically illustrated in Figure 5. Length and width increased most rapidly during the early part of the developmental stage. The increase in thickness, however, continued gradually up to the eleventh day, when 98.0 per cent of the final thickness was reached. Maximum thickness was recorded on the thirteenth day, with a sharp decline immediately following. The rapid falling off was in part due to kernels that were injured by heat on July 16. This was a very warm day and the sample gathered on the fourteenth day after pollination, July 17, showed the effect of the previous day's heat, as indicated by the measurements in Table II. A few of the kernels were distinctly flattened and the average thickness was lowered. While this affected some of the kernels, the majority had so nearly reached the ripe stage that the heat is thought not to have materially affected any of the results, as immature kernels were injured most severely. In addition to flattening, the kernels wrinkled and creased deeply and became firm and brittle. This is an indication that one might expect a decrease in yield if heat occurs during the early developmental stage. The more immature kernels in the lower whorls showed greater injury.

During the damp weather following the warm period, there was a tendency for the kernels with wrinkles to fill out, until finally most of them presented an appearance difficult to differentiate from natural ripening. The final appearance of a few kernels not thicker than the average during the first few days after pollination indicated that, in all probability, they did not recover from the premature desiccation.

Changes Within the Kernels

From the standpoint of knowing when to cut the crop for maximum yield and quality, it is desirable to understand the changes in green and dry weight, ash, and nitrogen content.

TABLE III

Daily Determinations of Green and Dry Weight, Ash, and Nitrogen of Gopher Oat Kernels

Date	Days after pollination	Determinations on twenty primary kernels with hulls removed							Determinations on about fi t kernels with hulls removed		Stage of development of kernels
		Green weight	Dry matter	Dry matter per cent of maximum	Dry matter	Moisture	Weight of ash	Ash on dry matter basis	Dry weight used for nitrogen determinations	Nitrogen on dry matter basis	
		grams	grams	per cent	per cent	per cent	grams	per cent	grams	per cent	
July 4	1	0.0569	0.0129	3.2	22.67	77.23	0.0004	3.10	0.1055	6.94	
5	2	.0960	.0200	5.0	20.83	79.17	.0007	3.75	0.0750	9.33	
6	3	.1960	.0401	10.0	20.45	79.55	.0011	2.74	0.1950	4.24	
7	4	.2477	.0558	13.9	22.52	77.48	.0011	2.06	0.2450	3.77	
8	5	26.20	.0594	14.8	22.67	77.33	.0012	2.10	0.3712	4.38	
9	6	.3429	.0866	21.6	25.25	74.75	.0021	2.42	0.6995	4.20	Early milk
10	7	.4201	.1188	29.7	28.27	71.73	.0039	3.28	0.7417	4.00	
11	8	.5099	.1638	40.9	32.12	67.88	.0049	2.99	0.8685	3.88	First yellow color
12	9	.5877	.2152	53.8	36.61	63.39	.0059	2.74	0.8300	4.22	Late milk
13	10	.6217	.2428	60.7	39.05	60.95	.0079	3.25	1.4364	4.10	General yellow color
14	11	.6544	.2762	69.0	42.20	57.80	.0086	3.11	1.4774	2.40	Early dough
15	12	.6343	.2696	67.4	42.50	57.50	.0090	3.33	1.8464	2.60	
16	13	.6900	.3533	88.3	51.20	48.80	.0086	2.43	2.0544	2.70	Dough
17	14	.5952	.3484	87.1	58.53	41.47	.0090	2.58	1.5534	2.98	
18	15	.6632	.3882	97.0	58.53	41.47	.0089	2.29	1.8150	2.58	First ripe
19	16	.5697	.3793	94.8	66.57	33.43	.0094	2.47	1.5900	3.18	
20	17	.5464	.3963	99.0	72.52	27.48	.0094	2.37	1.5934	2.96	General ripe
21	18	.4937	.3949	98.7	79.98	20.02	.0094	2.39	2.2735	3.00	
22	19	.5206	.3994	100.0	76.71	23.29	.0094	2.36	1.8432	2.60	
24	20	.4633	.3702	92.5	79.90	20.10	.0095	2.56	2.1664	2.90	
24	21	0.4672	0.3668	91.7	78.51	21.49	0.0094	2.56	2.0172	2.56	

Green weight.—Each sample of twenty kernels was weighed immediately after the physical measurements were determined. The daily weights are given in Table III, column 2, and the trend is illustrated graphically in Figure 6. During the first eleven days, the green weight of twenty kernels increased rapidly, with an average daily increment of 0.0543 gram. The graph indicates that this was practically a straight-line increase. Maximum green weight was reached on the thirteenth day and after the fifteenth day there was a pronounced decline.

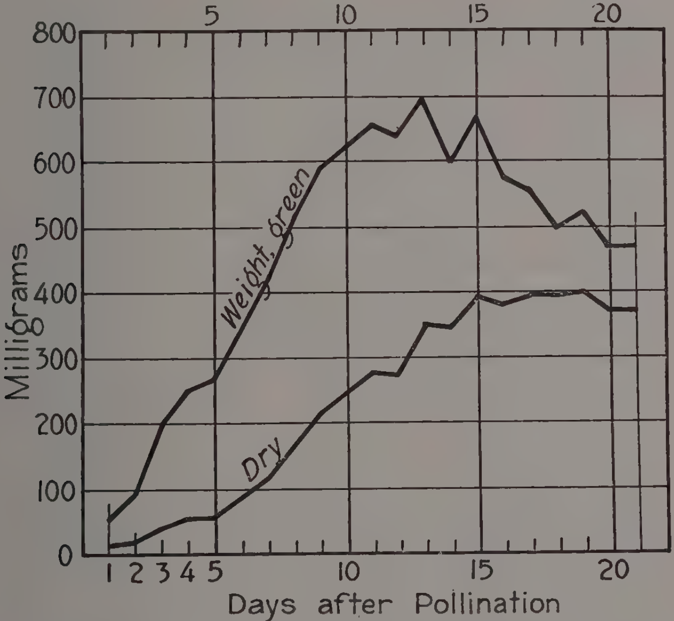

Fig. 6. Daily Green (Wet) and Dry Weights of Twenty Kernels After Removal of Hulls, from the Day After Pollination Until Maturity

Dry matter.—The actual dry matter content of the kernels increased uniformly up to the fifteenth day after pollination. At this time, twenty kernels, with the hulls removed, contained 0.3882 gram of dry matter. The final dry weight, on the nineteenth day, was 0.3994 gram. The actual dry weight should not be confused with the percentage of dry matter. During the ripening period, moisture was lost rapidly, and as a result the percentage of dry matter increased after the actual accumulation of dry matter ceased. The figures in Table III indicate this clearly. In column 3 the actual dry weights are given; in column 5, the percentage of dry matter for the same day. From the seventeenth to the eighteenth day, the actual amount of dry matter decreased slightly, but the percentage increased from 72.52 to 79.98 on the eighteenth day. On the nineteenth day the dry matter content was 76.71 per cent; on the following days it was 79.9 and 78.51 per cent, respectively. The changes in green and dry weight are illustrated graphically in Figure 6. The increase in dry matter was slow during the first five days but rapid from the fifth to the fifteenth day. After the fifteenth day, when the first ripe kernels were noted within the group used in this study, the total dry matter content remained nearly constant up to the twentieth day, when there was a tendency to decrease 8.3 per cent of the maximum amount with delayed harvesting. Harlan (8) and Kedzie (17) found a similar, tho longer, trend in the increment of dry matter in barley and wheat.

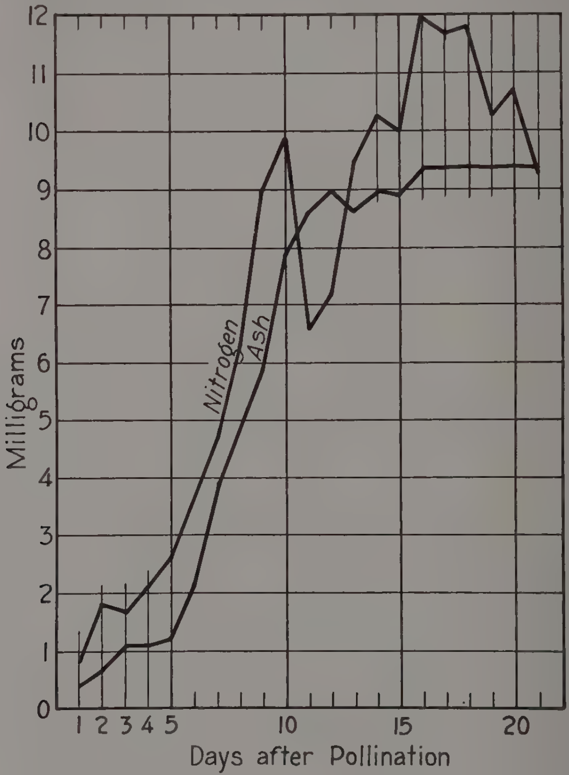

Fig. 7. Daily Weight of Nitrogen and Ash in Twenty Primary Kernels of Gopher Oats with the Hulls Removed, from the Day After Pollination Until Maturity

Ash content.—Ash was stored slowly during the first five days and then very rapidly until the twelfth day. The daily content of twenty kernels with the hulls removed is given in Table III, column 7, and graphed in Figure 7. On the fifth day there was 0.00125 gram in twenty kernels. This had increased to 0.0090 gram on the twelfth day, the increase per day being fairly uniform. There was a slight increase during the ripening period and no tendency for the amount of ash to decrease with delayed harvesting.

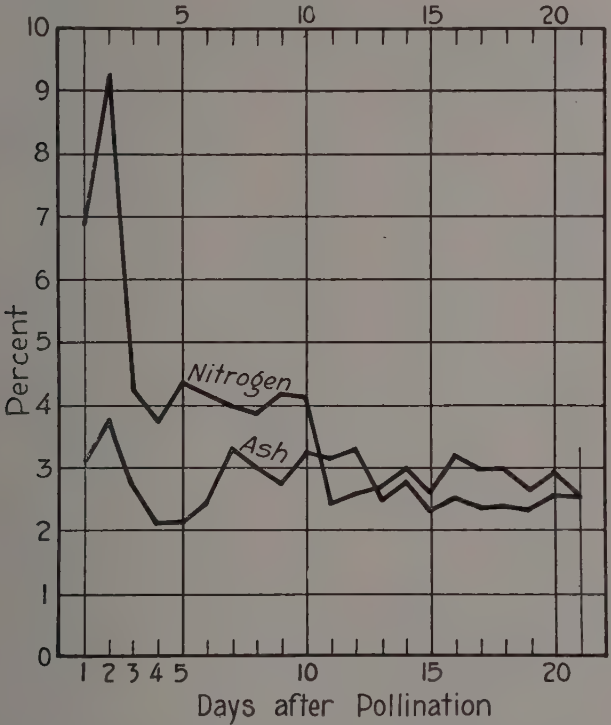

Fig. 8. Daily Change in Nitrogen and Ash Content Expressed in per Cent of Dry Matter

The proportion of ash expressed on a percentage basis was relatively high during the first few days after pollination, as illustrated graphically in Figure 8. The highest percentage was recorded on the second day. The proportion of ash remained high until the kernels reached the dough stage. There was 2.37 per cent of ash at the normal harvesting period.

Nitrogen content.—The problem of determining the total nitrogen in the first samples obtained was difficult. The dried kernels were extremely small and many were required for analysis. Each day's sample contained about fifty kernels, from which the hulls were removed at the time of analyzing. The weight of the air-dried kernels with the hulls removed was ascertained and then the actual nitrogen in the given weight was determined. The weight of kernels with hulls removed is given in Table III, column 9. Fine sand was mixed with the samples before grinding and the nitrogen content was determined by the Kjeldahl method. The values given may be regarded only as close approximations, owing to the large error involved in making the chemical determinations on relatively small samples. The size of the samples increased from 0.075 gram in the first few days to 1.5934 grams when the kernels were mature.

The nitrogen percentage of each dry weight is given in column 10 and graphed in Figure 8. The air-dried sample two days after pollination contained 9.33 per cent of nitrogen and at the normal harvesting period, 2.96 per cent.

To determine the location of the line in Figure 7 that indicates the trend in nitrogen content, the dry weight of twenty kernels with the hulls removed was multiplied by the percentage of nitrogen in the larger sample for the respective day. The graph, therefore, represents the calculated content of nitrogen in twenty kernels. The actual quantity found in the first few days was only a fraction of the total amount laid down. The increase was very rapid and fairly regular from the first to the tenth day. From the thirteenth to the sixteenth day a further increase in nitrogen is indicated, and after this date some loss with delayed harvesting.

Relationship Between External and Internal Characters

A detailed study of the relationship between external appearance and internal development was not a part of this investigation but careful notes on the changes in the appearance of kernel and floral parts were recorded. These observations are given along with the laboratory determinations to illustrate the relationship between internal and external evidences of maturity. The following is a brief summary of the field notes and laboratory determinations. The laboratory data on which the summary is based are included in Tables II and III and illustrated in Figures 2 to 8.

One day after general pollination of the kernels used in this study and four days after pollination in the apical spikelet: Pollination incomplete in the lower whorl. No marked change in the size of the ovary since previous day.

Two days: Marked increases in physical measurements, in green weight, and in nitrogen and ash content. Time of maximum percentage of nitrogen and ash.

Three days: Very rapid increases in length, width, green and dry weight, and in ash content. Marked falling off in the percentage of nitrogen and ash.

Four days: Pollination incomplete in lower whorl. Rapid increase in length, thickness, green and dry weight, and in nitrogen content. Slow gains in width and in ash content. Low point in percentage of ash.

Five days: Pollination complete in all florets of lower whorl. First trace of milky color in the endosperm of kernels in middle whorl. Rapid increases in length and in nitrogen content. Slow gains in width, green and dry weight, and in ash content.

Six days: End of the period of rapid increase in length. Rapid gains continued in thickness, green and dry weight, and in nitrogen and ash content. Percentage of ash established as at maturity. Width not increasing.

Seven days: Slow increase in length. No change in width. Marked increases in thickness, green and dry weight, and in nitrogen and ash content.

Eight days: Marked increases in length, thickness, green and dry weight, and in nitrogen and ash content. First trace of yellow in the pericarp.

Nine days: Slow gain in length. Rapid gains in width, thickness, green and dry weight, and in nitrogen and ash content. Distinct yellowing of kernels. Pericarp could be peeled free from seed. Late milk stage.

Ten days: Slow gains in length and width. Rapid gains in thickness, green and dry weight, and in nitrogen and ash content. Last date on which there was a high percentage of nitrogen. First trace of yellow in the glumes of the apical spikelets.

Eleven days: Slow gains in length, thickness, and width. Rapid gains in green and dry weight and in ash content. Percentage of nitrogen established as at maturity. Early dough stage. Lower leaves browning off. A few kernels showed a distinct amber color.

Twelve days: No gains in length or thickness. Maximum width attained. Temporary decline in green and dry weight. Upper spikelets showing a straw color. The stems were also distinctly lighter in color.

Thirteen days: First decided appearance of ripening in spikelets. Maximum thickness and green weight. Gains in length and dry matter. Beginning of decline in width. Kernels in dough stage, most of them amber color.

Fourteen days: Decline in width, thickness, and green and dry weight. Slight gain in length. Some kernels shriveled by heat. Kernels of middle whorl in late to hard dough stage. Apical kernels ripe. Kernels of lower whorl in late milk stage.

Fifteen days: Maximum length reached. Rapid decline in green weight after this time with no material increase in dry matter. A few of the glumes in the apical spikelets completely straw color with some of the glumes of spikelets in the middle whorl about half turned. First ripe kernels in middle whorl.

Sixteen days: Late to hard dough stage. Maximum nitrogen content with no material change in ash content after this date. A rather steady decline in physical measurements and green weight after this time. With the exception of an occasional light green glume, about 50 per cent of each glume surface of the spikelets used in this study was straw color.

Seventeen days: First noticeable hardening of lemma and palea. Ordinary harvesting period. Moisture content of primary kernels of the group studied, 27.48 per cent. A few of the kernels in the lower whorl still in dough stage. Slight increase in dry weight.

Eighteen days: Endosperm of all primary kernels mealy. Moisture content of the primary kernels of the group studied, 20.02 per cent. In the lower whorls, glume surface still 25 to 50 per cent green, the palea having a green edge.

Nineteen days: Maximum actual dry weight and a decline with further ripening after this date. About 95 per cent of the glume surfaces in the middle whorl straw color. Some green in lower whorl. Past usual cutting time. Kernels completely ripe. Moisture 23.29 per cent.

Twenty days: Declines in all physical measurements and actual green and dry weights. Moisture 20.10 per cent.

Twenty-one days: Slight changes.

Application of Daily Growth Study to Farm Practices

The time required for complete pollination within the panicle has a direct bearing upon the harvesting period. There was a tendency for later kernels to develop rapidly, but uneven ripening within the panicle was the rule. Ripening in the spikelets followed in the same order as pollination, from the apex downward. The yield and quality must be influenced by the filling and ripening of the kernels in the lower whorl.

It is apparent from the data in Tables II and III that the maximum physical size of the kernel was attained at about fifteen days after pollination and the dry matter content at this stage of development was within 3 per cent of the maximum. This was considered the end of the developmental period. Only a few of the usual indications of ripening were apparent at this time. The developmental stage was followed by a period of about four days during which the entire plant ripened rapidly and the actual weight of dry matter increased 3 per cent. During this period only slight increase in yield could be expected from delayed harvesting, but the appearance of the threshed grain improved as the green faded out of the lemma and palea. There was an indication of a slight loss in total dry matter and nitrogen content with over-ripening.

The moisture content was reduced to about 20 per cent one day after the estimated usual time of harvesting. Considering that some rain fell on each of the two previous and the three following days, and that the sample, still wet with dew, was gathered before seven o'clock in the morning, the moisture percentage of the kernels during the last four days was low.

EFFECT ON GERMINATION OF IMMATURITY AND CONTROLLED LOW TEMPERATURES

The effect on germination of immaturity and controlled low temperatures was investigated at the same time as the study of kernel development.

Materials and Methods

Three varieties of oats were used in the study—Gopher, Banner, and Victory. The three were grown side by side in one of the variety test blocks at University Farm. The plots were 8 feet wide and 134 feet long. The oats were seeded with an ordinary drill on April 10. A border, consisting of two outside drill rows on each side and a one-foot swath at the ends, was removed before sampling. The plot of Gopher oats used in the study of daily development was included in the same group, altho seeded ten days later.

The soil and seasonal climatic conditions have been described. The details of precipitation and temperature are given in Table I.

Gopher oats was ripe on July 16, Victory on July 23, and Banner on July 22. Yields for the season and long-time averages are as follows: Gopher 1926, 34.1 bushels; 1921-27 average, 58.5 bushels. Victory, 1926, 39 2 bushels; 1921-27 average, 58.4 bushels. Banner, 1926, not included in variety trials. Gopher, 1926, average straw length 24 inches. Banner and Victory, 1926, average straw length 30 inches.

In the study of daily development, it was observed that actual dry matter content of the kernels was closely correlated with maturity. Therefore, to check the maturity of the samples, it was necessary to determine the dry matter content each day. Check samples of approximately ten representative panicles of each variety were used for this purpose. The procedure in each case was the same but the varieties were kept separate. After discarding the immature spikelets, as mentioned on page 11, thirty primary kernels were selected at random from the group. These were hulled, weighed immediately, dried for twenty-four hours at 204.8°F. (96°C.) and then re-weighed to determine the dry matter content. After further drying, the sample was again weighed to check the accuracy of the first figure.

Technic of Exposure to Controlled Low Temperatures

Each day from July 8 to 23, samples for exposure to controlled temperatures were gathered in the morning, between six and seven o'clock. The equivalent of a large binder sheaf of each variety was harvested by pulling the oats at six distributed areas in the plot. With the roots attached, the plants of each variety were wrapped separately in a damp cloth before they were taken from the field.

In the laboratory, each large sheaf was spread out on a long bench and groups of heads were selected at random throughout the length of the bench to make up smaller sheaves. The large sheaf was thus split into seven smaller ones. Six of these were subjected to various freezing temperatures and the seventh was used as a check.

In addition to the eighteen small sheaves, three lots of Gopher oats growing in pots were subjected to controlled temperatures each day. After exposure in the low-temperature chamber the pots were reset in the field, where they had been placed at seeding time in the spring. The other samples were grouped together each day in two cotton bags with the checks included and hung to dry in an airy place. Altho the early samples contained a high percentage of moisture, they dried thoroly with few exceptions. Early in the fall, the samples were taken to the seedhouse and stored in metal boxes. After threshing in December, the oats were placed in paper envelopes and stored in metal boxes in the Seed Laboratory during the winter months.

The desired temperatures were obtained by using a Lipman artificial refrigeration plant, consisting of an insulated chamber lined with coils in which liquid ammonia vaporizes. After expansion, the gas is drawn back by a pump located outside the chamber and is compressed and liquefied before recirculating in the coils. Vaporizing the liquid ammonia in the coils reduces the temperature in the insulated chamber and by continued operation temperatures as low as —40°F. (—40°C.) can be obtained. Hildreth (1926) described the machine briefly.

The insulated chamber was enclosed in a small booth as a further precaution in maintaining the temperature. A thermograph, two minimum thermometers, and a fan were enclosed in the freezing chamber. The fan kept the cool air in rapid circulation.

The temperatures were maintained by Harvey thermo-regulators within a range of ±0.54°F. (±0.3°C.) when the machine was operating smoothly. The electric light bulb in the fan circuit burned out repeatedly on July 8, allowing the temperature to fall to 23°F. (—5°C.) on three occasions, in all, about fifteen minutes. The thermo-regulator was changed on July 18 and the temperature of 31°F. (—0.5°C.)

fell to 22° to 25°F. (−5.6° to −3.9°C.) for half an hour before being noticed. On July 19 a temperature control of 26°F. (−3.3°C.) was used for two hours instead of 29° and 27°F. (−1.7° and −2.7°C.).

The small sheaves were placed on wire shelves in the chamber with space between to allow free movement of air. Care was taken to prevent any of the material touching walls, pipes, or temperature control. A check on the time required to readjust the temperature after the doors had been opened showed that at each sixty-minute change of temperature and samples three to five minutes was required to cool off. In interpreting results, it should be remembered that this adjustment period formed part of the sixty minutes at any given temperature.

The treatments to which the samples were subjected have been grouped below according to severity. Equal numbers of samples of Gopher, Victory, and Banner oats were subjected to each treatment.

Group A. Cooled two hours at 35°F. (1.7°C.). Exposed one hour at 31°F. (−0.5°C.).
AA. No pre-cooling. Exposed one hour at 31°F. (−0.5°C.).
Group B. Cooled two hours at 35°F. (1.7°C.). Exposed one hour at 31°F. (−0.5°C.) and then an additional hour at 29°F. (−1.7°C.).
BB. No pre-cooling. Exposed one hour at 29°F. (−1.7°C.).
Group C. Cooled two hours at 35°F. (1.7°C.). Exposed one hour at 31°F. (−0.5°C.), one hour at 29°F. (−1.7°C.) and then an additional hour at 27°F. (−2.7°C.).
CC. No pre-cooling. Exposed one hour at 27°F. (−2.7°C.).
Group D. Check samples, neither cooled nor subjected to freezing temperatures. Dried with the other samples each day.
Group E. Conducted only on July 13. Cooled two hours at 35°F. 1.7°C.). Exposed one hour at 31 to 30°F. (−0.5 to −1.1°C.), and then two hours at 27°F. (−2.7°C.).
EE. No pre-cooling. Exposed two hours at 27°F. (−2.7°C.).

Groups AA, BB, CC, and EE were stored in the laboratory wrapped in a damp cloth while the other samples were cooled. They were therefore exposed to the low temperatures without any previous cooling.

The machine was in operation from 8 a.m. to 1 p.m. each day. Starting at 8 o'clock, the chamber was maintained at 35°F. (1.7°C.) for two hours with all the samples of groups A, B, and C in the chamber. The three pots of Gopher oats were also included. At 10 a.m. the temperature was reduced to 31°F. (−0.5°C.) and the samples in group AA were added to those in the chamber. One pot of Gopher oats and the samples in groups A and AA were removed at 11 o'clock. Simultaneously group BB was inserted and the temperature was reduced to 29°F. (—1.7°C.). At 12 o'clock the second pot of Gopher oats and the samples in groups B and BB were removed. Group CC was immediately placed in the chamber and the temperature was reduced to 27°F. (—2.7°C.) and maintained for one hour. The last samples were removed at 1 p.m.

Groups E and EE consisted of samples subjected to temperatures slightly different from those previously mentioned and included only on July 13. Group E was pre-cooled for the usual two-hour period at 35°F. (1.7°C.) and exposed one hour at 30 to 31°F. (—1.1 to —0.5°C.). Group EE was not pre-cooled. Both groups were held at 27°F. (—2.7°C.) for two hours.

All samples exposed to the temperature of 31°F. (—0.5°C.) on any one day were in the cooling chamber together between the hours of 10 and 11 o'clock in the morning. All samples for the day reported exposed to 29°F. (—1.7°C.) were in the chamber from 11 o'clock until noon. The results for any one day as between varieties exposed at the same temperatures are, therefore, directly comparable.

After the samples were removed from the chamber, they were stored in the outer booth at a temperature ranging from 61° to 65°F. (16.1° to 18.3°C.) until the middle of the afternoon. Facilities were not available to duplicate the natural transitions in temperature of an autumn morning, but the test was probably more severe than field conditions.

The samples in Group C were subjected to what might be considered an early fall frost, being chilled for two hours at a temperature just above 32°F. (0°C.). They were then maintained at lowering temperatures of 31° F. (—0.5° C.), 29° F. (—1.7° C.), and 27° F. (—2.7° C.) for three hours. The change back to normal temperatures while protected from the sun also approached field conditions as nearly as possible.

Germination Tests

Laboratory germination tests were conducted by the State Seed Laboratory. All samples were germinated in duplicate for seven days before counting.

Field germination was tested by seeding 100 kernels in one of the variety trial plots in the spring of 1927 about a week after it was possible to work the land. The field reading was made between the third and fourth weeks and later germination, if any, was disregarded. Wright (1921) pointed out that in field germination tests the seedlings were counted and then pulled out at the end of about three weeks. Only an occasional weak sprout appeared after the first count.

Laboratory Germination of Samples Exposed to Controlled Low Temperatures

The first samples of Gopher oats subjected to temperatures ranging from 35°F. (1.7°C.) to 27°F. (—2.7°C.) were in the late milk to early dough stage. Samples were exposed daily from this time to complete maturity. A study of the laboratory germination during the first five-day period, July 8 to 12, as summarized in Table IV, indicates that the exposed samples germinated about as uniformly as the checks. The mean germination of the check samples, group D, line 1, was 93.4 per cent, as compared to a range in germination from 84.6 to 96.2 per cent for the exposed samples, groups A to CC inclusive, line 1. There is a noticeable difference between the average germination of group B, line 1, and the check sample, group D, line 1. The exposed sample, group B, line 1, had an 8.8 per cent lower germination than the average for the checks. The importance of this difference is minimized because the average germination of the sample receiving the same treatment and an additional hour at 27°F. (—2.7°C.) was 92.2 per cent, group C, line 1, and this germination is within 1.2 per cent of the check. The significance of this difference has been determined by Student's method. The odds that the low-germinating sample and the check are significantly different in germination are approximately 9.82:1. In the second five-day period, July 13 to 17, the mean germination of the checks, group D, line 3, was 97.4 per cent; that of the exposed samples, groups A to CC inclusive, line 3, ranged from 98.2 to 99.2 per cent. The differences in average germination between the first and second five-day periods indicate that lower germinating power in the early samples was due to immaturity. During the third five-day period, from July 19 to 23, there was no material change from the figures reported in the second period. Apparently the temperatures to which Gopher oats were exposed had no consistent effect on germination.

Samples of Victory oats were subjected to the controlled temperatures daily through the stages from early milk to complete maturity. Both Victory and Banner oats were less mature when the first samples were taken and had a lower germination than Gopher oats. The laboratory germination of the untreated samples of Victory oats indicates reduced viability during the milk stage. The mean germination of the check samples, group D, line 11, for the first five-day period, July 8 to 12, which included the milk stage, was 70.8 per cent. The exposed samples, groups A to CC inclusive, line 11, ranged from 72.8 to 85.4 per cent for the same period. During the second period, from July 13 to 17, the checks, group D, line 13, averaged 98.2 per cent germination, with a range of 91.5 to 95.8 per cent for the exposed samples, groups A to CC inclusive, during the same period. The germination of the checks, group D, line 15, during the third period, from July 18 to 23, was 98.4 per cent, with the mean germination of the exposed samples, groups A to CC inclusive, ranging from 95.6 to 99.0.

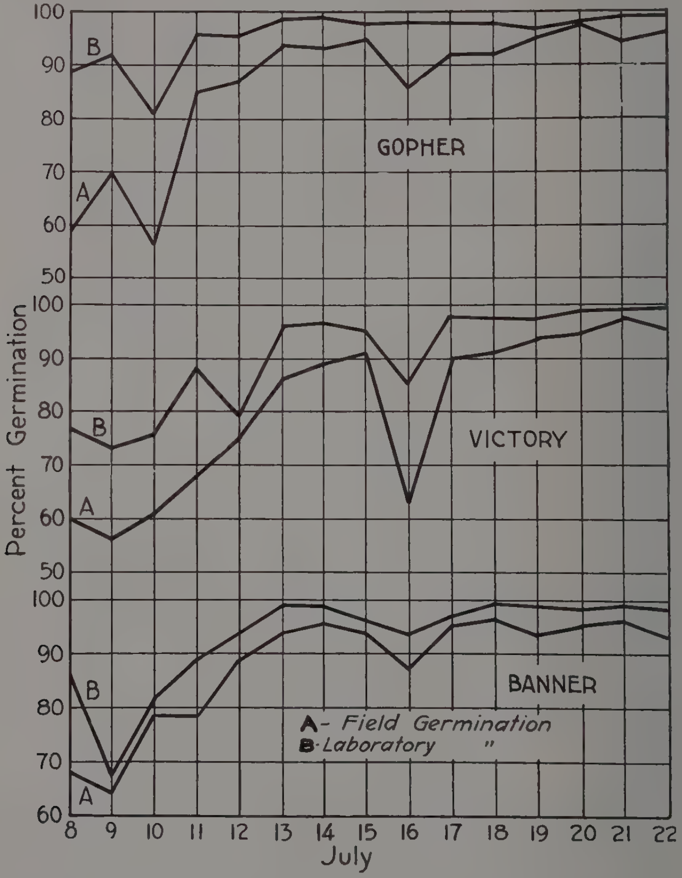

Fig. 9. Comparison of Mean Germination of Gopher, Victory, and Banner Oats

The upper line B in each group is the laboratory germination; the lower line A is the field germination.

Banner oats, also, was exposed to controlled temperatures daily from the early milk stage to complete maturity. There was considerable irregularity in the germination of the samples harvested during the milk stage. The mean germination of the checks, group D, line 21, during the first five-day period, from July 8 to 12, was 82.6 per cent and for the second period, line 23, 97.2. The difference in germination for the two periods is 14.6 per cent and is attributed to the

Variety and period	Method of making germination	Group A 2 hr. at 35°F. (1.7°C.) 1 hr. at 31°F. (−0.5°C.)	Group B 2 hr. at 35°F. (1.7°C.) 1 hr. at 31°F. (−0.5°C.) 1 hr. at 29°F. (−1.7°C.)	Group C 2 hr. at 35°F. (1.7°C.) 1 hr. at 31°F. (−0.5°C.) 1 hr. at 29°F. (−1.7°C.) 1 hr. at 27°F. (−2.7°C.)	Group AA 1 hr. at 31°F. (−0.5°C.)	Group BB 1 hr. at 29°F. (−1.7°C.)	Group CC 1 hr. at 27°F. (−2.7°C.)	Group D check no treatment	Line
Gopher		per cent	per cent	per cent	per cent	per cent	per cent	per cent	
First 5 days.......	Lab.	89.2	84.6	92.2	91.6	96.2	91.6	93.4	1
July 8-12	Field	71.0	65.6	72.0	70.8	74.4	75.8	74.2	2
Second 5 days.....	Lab.	99.2	98.5	98.6	98.2	98.5	98.4	97.4	3
July 13-17	Field	91.0	94.5	92.8	92.4	91.0	90.2	91.1	4
Third 5 days*.....	Lab.	97.2	99.0	97.6	99.2	99.0	97.0	97.6	5
July 18-23	Field	91.6	97.4	97.4	97.0	93.8	94.0	97.2	6
15-day average	Lab.	95.2	93.7	96.1	96.3	97.8	95.6	96.1	7
Probable error......	....	±1.450	±2.024	±0.848	±1.133	±0.758	±0.897	±0.752	8
15-day average	Field	84.5	85.2	87.4	86.7	86.7	86.6	87.4	9
Probable error......	....	±2.418	±3.202	±2.632	±2.528	±0.848	±1.886	±2.662	10
Victory									
First 5 days.......	Lab.	85.4	80.8	81.6	76.4	72.8	77.4	70.8	11
July 8-12	Field	68.6	67.4	66.6	61.6	63.4	60.4	66.4	12
Second 5 days.....	Lab.	95.8	91.5	93.2	95.4	92.5	95.2	98.2	13
July 13-17	Field	84.8	78.5	83.6	88.6	79.5	86.8	88.2	14
Third 5 days.......	Lab.	98.2	99.0	98.8	98.0	99.0	95.6	98.4	15
July 18-23	Field	95.4	96.4	93.0	95.6	96.8	84.2	92.4	16
15-day average	Lab.	93.1	90.3	91.2	89.9	87.7	89.4	89.7	17
Probable error......	....	±1.261	±2.090	±1.989	±1.979	±3.235	±2.445	±3.026	18
15-day average	Field	82.9	80.9	81.0	81.9	79.9	75.2	82.3	19
Probable error......	....	±2.479	±3.321	±3.434	±2.829	±3.534	±3.284	±2.681	20
Banner									
First 5 days.......	Lab.	78.6	90.0	80.6	84.0	81.0	85.6	82.6	21
July 8-12	Field	69.4	72.8	68.4	75.4	71.0	73.4	71.8	22
Second 5 days.....	Lab.	97.2	98.7	97.6	98.0	91.7	95.0	97.2	23
July 13-17	Field	95.6	97.7	92.2	92.0	86.2	93.2	91.0	24
Third 5 days.......	Lab.	98.8	98.2	98.2	98.6	98.8	99.0	99.2	25
July 18-23	Field	91.0	95.6	97.0	95.1	92.4	95.6	97.2	26
15-day average.....	Lab.	91.5	95.4	92.1	93.5	90.4	93.2	93.0	27
Probable error......	....	±2.352	±1.336	±1.972	±1.824	±1.990	±1.472	±1.834	28
15-day average	Field	85.3	88.0	85.8	86.6	84.1	87.5	86.6	29
Probable error......	....	±2.594	±2.717	±2.643	±2.001	±2.456	±2.294	±2.537	30

* July 21 omitted.

difference in maturity. The laboratory germination failed to bring out any conclusive evidence of injury due to the temperatures applied.

The groups of samples designated E and EE, on page 29, were subjected to more severe conditions. All three varieties were included in this test on July 13. The Victory and Banner samples contained 39.1 and 44.6 per cent dry matter, respectively, and the Gopher sample 66.1 per cent. The first two varieties were in the milk stage; the last was in the dough stage. The average germination of the exposed samples was similar to that of the checks.

The other changes in the temperature of the chamber mentioned on page 29 seemed to have no effect upon germination. Even with the temperature as low as 26°F. for two hours on July 19, no material effect could be detected.

Field Germination of Samples Exposed to Controlled Low Temperatures

A direct comparison of the laboratory and field germinations is made possible by the arrangement of the data in Table IV. Two lines are used to set forth the average germinations by five-day periods. In the upper line in each case are given the laboratory results and immediately below, in the respective columns, are the field germinations representing the same lots of grain.

In every average reported in Table IV the germination was lower in the field than in the laboratory. The differences were greater in the immature samples with the exception of Banner oats.

The first five-day mean germination of the check samples, group D, line 2, of Gopher oats for July 8 to 12, was 74.2 per cent. The range in the exposed samples, groups A to CC, line 2, was from 65.6 to 75.8 per cent for the same period. The low germination percentage of 65.6 for the sample, group B, line 2, as compared with another with a more severe treatment, group C, line 2, is similar to the results for the laboratory tests of the oats subjected to these treatments.

In the second five-day period, the germination of the checks, group D, line 4, was 91.1 per cent and the range in the exposed samples, groups A to CC, from 90.2 to 94.5. There was an increase of 16.9 per cent in the average germination for all groups for the second period over the first. The germination in the third period was still higher, the checks, group D, line 6, averaging 97.2, and the exposed samples, groups A to CC inclusive, line 6, varying from 91.6 to 97.4. These results indicate no appreciable injury as a result of being exposed to low temperatures. However, the germination was highest in the samples that were fully mature.

During the first five-day period the field germination of Victory oats was lower than that of Gopher or Banner. The average germination of the checks, group D, line 12, was 66.4 per cent and the range in the exposed samples, groups A to CC inclusive, line 12, from 60.4 to 68.6. The germination in the non-cooled groups, AA, BB, and CC, ranged from 60.4 to 63.4 per cent, line 12. This is one of the widest variations between checks and exposed samples. Even in this case some of the individual lots germinated higher than the checks. In the second five-day period the checks, group D, line 14, germinated 88.2 per cent and the exposed samples, groups A to CC inclusive, line 14, varied from 78.5 to 88.6 per cent. Groups B and BB, line 14, had a materially lower germination than the checks. Groups C and CC, line 14, with a more severe treatment, germinated nearly as high as the checks. It is again evident, altho with a different variety, that the germination was higher in the second five-day period than in the first, the average difference being 21.8 per cent. The checks, group D, line 16, germinated 92.4 per cent during the third five-day period, with a range of 84.2 to 95.8 per cent in the exposed samples. These samples were more nearly mature than those in the previous five-day period and had a higher average germination of 4.2 per cent.

The field germination of Banner oats during the early stages of development was similar to that of Gopher. The mean germination of the checks, group D, line 22, during the first five-day period, was 71.8 per cent and the range in the exposed samples for the same period from 68.4 to 75.4. In the second five-day period the checks, group D, line 24, averaged 91.0 per cent and the exposed samples varied from 86.2 to 97.7 per cent. During the third five-day period, when the oats were approaching maturity, the checks, group D, line 26, averaged 97.2 per cent, and the exposed samples ranged from 91 to 97 per cent. There was an increase of 19.2 per cent in the average germination in the second five-day period as compared with the average for the first period and a further increase of 6.2 per cent in the third period. There was no consistent evidence of freezing injury.

There was a distinct difference in the appearance of the seedlings produced by the different lots of seed. This was true for all varieties. The kernels harvested in the milk stage produced seedlings that were slender and pale green. They germinated quickly but less vigorously and grew less rapidly during the first few days. Kernels that were harvested in the dough stage produced seedlings that were dark green, broad-leaved, and vigorous. The differences were not so great at the end of ten days. These results agreed with the observations recorded for barley, corn, and wheat by Harlan (1922), Alberts (1926), and Crozier (1895).

Comparison of Fifteen-Day Average Germinations

The mean laboratory and field germinations for the fifteen-day period have been included in Table IV. Some means that show the widest variations have been selected to illustrate the lack of significant differences in germination between samples subjected to the various treatments. The mean germinations and differences are as follows:

Group	Line	Germination of exposed samples	Germination of checks	Difference in germination	Difference / Probable error
		per cent	per cent	per cent	
B	7	93.7±2.024	96.1±0.752	2.4±1.496	1.6
CC	19	75.2±3.284	82.3±2.681	7.1±1.650	4.3
BB	27	90.4±1.990	93.0±1.834	2.6±0.941	2.8
BB	29	84.1±2.456	86.6±2.537	2.5±2.131	1.1

The probable error of the difference was calculated by using the formula $\sqrt{Ea^2+Eb^2-2rabEaEb}$ where a and b represent the probable errors of the two germination percentages compared. The difference in germination between group CC, line 19, and the check amounts to 7.1±1.650 with odds of 267.1:1. This is a significant difference, according to the usual interpretation of statistical data. The importance of this difference is minimized, however, by the fact that similar samples, line 9, group C, exposed to more severe temperatures showed practically the same germination as the checks, line 19, group D. The other three differences, reported above, are not significant according to the usual interpretation of statistical data.

In Table V, which is a condensed summary of the averages as given in Table IV, percentages of laboratory and field germination have been grouped according to treatment before subjecting them to freezing temperatures and are given for each variety. The checks are included as a separate group. A direct comparison of average germinations is made possible by the method of exposing the samples. With the exception of one day, when only two samples were included, three different lots of each variety were exposed to different temperatures on each of fifteen days. The averages in Table V, therefore, were derived from the germination of forty-four samples, with the exception of the checks and the field germination of the non-cooled Victory oats. The averages reported in the check column are based on results from fifteen samples; the field germination of Victory oats represents an average of the results of forty-three samples instead of forty-four.

Samples of Gopher oats that were cooled and then subjected to various low temperatures had an average laboratory germination of 95.0±0.876 per cent. Similar samples that were not cooled before being subjected to the low temperatures averaged 96.5±0.543 per cent, while the checks, which were neither cooled nor exposed, averaged

96.1±0.752 per cent. The germination percentages for Banner and Victory samples showed similar close relationships. The differences between the mean germination of the samples subjected to the low temperatures and the checks are too small to be significant.

TABLE V

SUMMARY OF AVERAGE GERMINATIONS IN LABORATORY AND FIELD GIVEN IN TABLE IV

Method of germination and variety	Average germination of samples		
	Groups A. B, C, cooled and subjected to low temperatures	Groups AA, BB, CC not cooled but subjected to low temperatures	Group D, checks not cooled or subjected to low temperatures
	per cent	per cent	per cent
Laboratory			
Gopher	95.0±0.876	96.5±0.543	96.1±0.752
Victory	91.5±1.049	89.0±1.504	89.1±3.026
Banner	93.0±1.115	92.3±1.024	93.0±1.834
Field			
Gopher	85.7±1.599	86.6±1.088	87.4±2.662
Victory	81.6±1.794	79.0±1.864	82.3±2.681
Banner	86.3±1.530	86.0±1.303	86.6±2.537

If there had been a critical period in the development of the kernel, when it was more subject to injury from exposure to freezing temperatures, it should be evident in the comparison of the five-day averages in Table IV or the fifteen-day mean germinations in Table V. Similarly, if the degree of temperature or the duration of exposure was an influencing factor, it would be apparent by the same comparisons. There were no significant differences between the fifteen-day average germination percentages for the treated samples and the checks, but there was a pronounced increase in germination at the second and third five-day periods for each variety as compared with the average for the first period. This indicates that immaturity, instead of the low temperatures used, lowered the average germination.

Comparison of Laboratory and Field Germinations

The average laboratory germination of 264 exposed samples was 92.8 per cent as compared to 92.7 per cent for the 45 checks. The same 264 samples had an average germination in the field of 84.1 per cent as compared to 85.4 per cent for the 45 checks. When the laboratory germinations, 309 in number, are compared with those of the same lots tested in the field, germination is 8 per cent lower. As indicated in Figure 9, most of this difference can be accounted for by the spread between laboratory and field germination of immature samples. The differences in the germination at the five-day periods noted in Table IV, and the position of the lines in Figure 9, indicate that the widest variation between laboratory and field trials occurred during the early stages of kernel development. The average daily germination of the six samples exposed to low temperatures is graphed in this figure. The daily dry-matter content of the samples and notes on the stage of maturity are indicated in Table VI.

TABLE VI

Dry Matter Content and Notes on the Stages in Development of Samples Exposed to Controlled Low Temperatures

	Gopher		Victory		Banner	
Date	Dry matter	Stage of maturity	Dry matter	Stage of maturity	Dry matter	Stage of maturity
	per cent		per cent		per cent	
July 8	57.0	Milk to dough	34.9	Early milk	29.7	Early milk
9	55.5	Yellow kernels	33.8	....	33.2	
10	62.0	First ripe	33.0	Milk	34.7	Milk
11	63.8	Some hard	35.1	Late milk	36.6	Late milk
12	....	....	37.1	Early dough	39.7	Early dough
13	66.1	....	39.1	....	44.6	First yellow kernels
14	62.6	50 per cent hard	43.1	Dough	45.8	Dough
15	67.3	....	43.6	Yellow kernels	53.4	Late dough
16	72.6	Ripe	47.2	Late dough	52.9	Some hard
17	86.6	Dry, mealy	....	First hard	57.9	
18	86.6	....	63.1	....	66.5	50 per cent hard
19	80.7	....	59.6	....	66.5	
20	87.4	....	68.5	50 per cent hard	67.3	Some ripe
22	79.5	....	69.9	....	77.7	Ripe
23	84.9	....	79.1	Ripe	80.9	Ripe, mealy

There was a marked spread between field and laboratory germinations of Gopher and Victory oats during the early stages of development. The general trend of the two lines, in both these varieties, indicates that the field germination approaches the laboratory germination as the oats near maturity. The field germination, however, remains slightly lower. The samples of Banner oats showed no material difference between laboratory and field germinations, but no explanation of this could be discovered. The sudden dips in the lines on July 9, 10, 12, and 16 do not coincide with the dates when the samples were subjected to lower than the desired low temperatures.

The spread between laboratory and field germinations indicated in Figure 9 emphasizes the inadequacy of the laboratory test to determine the true germinating value of immature oat samples.

Throughout the trials, the difference in the stages of maturity between Gopher, Victory, and Banner oats masked any variety differences that may have existed. The averages in Table V and the graphs in Figure 9 indicate that the trend of response was similar.

Correlation Between Dry Matter and Germination

The correlation between dry matter and germination was computed by using the averages graphed in Figure 9 and the dry matter data from Table VI.

There was a decided correlation between the quantity of dry matter in the sample at the time of harvest and the germination. This was true in both laboratory and field germinations, but in the latter case the correlation was more pronounced, as indicated below.

	Gopher	Victory	Banner
Correlation between field germination and dry matter content................	0.70 ± 0.09	0.78 ± 0.06	0.74 ± 0.07
Correlation between laboratory germination and dry matter content............	0.59 ± 0.11	0.75 ± 0.07	0.64 ± 0.10

It is apparent from these data that there is a high correlation between field germination and percentage of dry matter. The above figures represent the correlation coefficient, altho the correlation ratio might have been used. Throughout the experiment, as indicated in Table VI, Gopher oats was the most mature and Victory the least, with Banner between. Owing to the earlier maturity and consequent higher dry matter content of Gopher oats, the correlation between dry matter and germination was lower for this variety than for Victory or Banner. It appears that dry matter, maturity, and germination are closely correlated.

EFFECT OF EXPOSURE TO LOW TEMPERATURES ON THE GREEN LEAVES AND STEMS OF IMMATURE OAT PLANTS

As a parallel study to the effect of frost on the viability of immature oat kernels, potted plants were used to study the effect of controlled low temperatures upon the plants themselves. The pots were exposed with the other samples to the regular temperatures listed on page 29 under groups A, B, and C, and kept from the sun in the booth surrounding the cooling chamber for about two hours before replacing them in the field.

The first pots of Gopher oats were exposed to the controlled low temperatures when the dry matter content of the kernels amounted to 26.6 per cent. According to the daily development study, this was the very early milk stage, six or seven days after pollination. Within twenty-four hours after being replaced in the field, they turned yellow and the stems began to break over. The stems of the plants exposed at 27°F. (—2.7°C.) crinkled much more freely and for a longer time than those exposed to 29°F. (—1.7°C.) and 31°F. (—0.5°C.). As the plants approached maturity, it was noticeable that fewer stems crinkled after being subjected to the low temperatures. From July 10 to 12, about 50 per cent of the plants exposed at 31°F. (—0.5°C.) and 29°F. (—1.7°C.) were injured in this way. During this time, the kernels were increasing in length and developing just enough starch to be considered in the milk stage. On the third day the kernels showed a dry matter content of 39 per cent, and only about 10 per cent of the culms of the plants exposed at 31°F. (—0.5°C.) and 29°F. (—1.7°C.) broke over from this time until maturity. The percentage of culms that crinkled when exposed at 27°F. (—2.7°C.) decreased from 90 to 50 per cent during the first six days. By this time the dry matter in the kernels had reached 50 per cent and from then to maturity only about 10 per cent of the stems crinkled. There was more injury to stems exposed to the lower than to the higher temperatures.

A record was also kept of the effect on the color of the leaves and stems of exposure to freezing temperatures. The three temperatures had the same effect and no green color remained in the plants until July 17, at which time the kernels contained 58 per cent dry matter. The chlorophyll was destroyed and within a few days gave the plants the appearance of uniform ripening. It was estimated that on the above date the plants retained about 5 per cent of the green color. There was an increase in the proportion of green color retained by the plants from this time until natural ripening began. Exposure to a temperature of 31°F. (—0.5°C.) was as injurious in destroying the chlorophyll as exposure to 27°F. (—2.7°C.).

SUMMARY AND CONCLUSIONS

The daily growth of the Gopher oat kernel was studied from pollination to maturity, and samples of Gopher, Victory, and Banner oats in the early milk to ripe stages were exposed to controlled low temperatures at daily intervals.

The average period of flowering in panicles lasted about eight days, progressing from the apex downward. The kernels in the lowest whorl were still in the late dough stage when the apical kernels were ripe.

Growth in length was most rapid during the first six days and then more gradual until the maximum was reached on the fifteenth day. Width and thickness increased rapidly during the first ten days and reached a maximum before growth in length ceased.

Green weight increased rapidly for thirteen days; after the fifteenth day there was a pronounced decline. Dry weight increased more gradually than green weight until ripening began, on the fifteenth day. Increase in actual dry matter during the ripening period was 3 per cent of the maximum amount, and the loss when harvesting was delayed two days was 8.3 per cent.

Nitrogen increased rapidly during the first ten days and ash during the first twelve days. After this there was considerable fluctuation in the amount of nitrogen in twenty kernels, as indicated by the curve, and very slight differences in the amount of ash.

The developmental period of the kernels used in this study continued for fifteen days after pollination and was concluded when the glumes of the apical spikelet became straw color. General ripening occurred in two days and was completed in four days, during which time the lemma and palea took on a uniform straw color and the moisture decreased from 41.47 to about 21 per cent.

Controlled temperatures ranging from 31° to 27°F. (—0.5° to —2.7°C.), extending over periods of from one to three hours, had no apparent effect on germination. This was true whether the samples were cooled for two hours before being exposed to low temperatures or were placed directly in the chamber without pre-cooling.

The average laboratory germination increased materially and the field germination to a still greater extent with the accumulation of dry matter in the kernels.

The average germination was higher in the laboratory than in the field. The laboratory germination of immature samples, with few exceptions, was relatively high and not a reliable indication of what results might be in the field.

The average laboratory germination of mature samples was always slightly higher than the field test, but was a reliable index of field germination.

The field germination of immature kernels was low and the seedlings lacked vigor.

During the developmental period, a temperature of 31°F. for one hour destroyed most of the green color in the plants of Gopher oats.

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Agricultural Experiment Station

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A NEW METHOD FOR ESTIMATING THE TRUE FAT CONTENT OF BUTTERMILK[1]

W. E. Petersen and E. O. Herreid

An accurate method for estimating fat in buttermilk has been a need of the dairy industry for some time. The fundamental reason for testing buttermilk is to determine the exhaustiveness of churning. This has been impossible with present methods.

Considerable discrepancy has been revealed in the past in comparing the different methods of testing buttermilk. Meyers (1891) apparently was the first to show that the Babcock method gives results considerably lower than ether-extraction methods. Chemists in the laboratory of the American Association of Creamery Buttermakers concluded that the Babcock method gave results too low for buttermilk as compared to the official Roese-Gottlieb method. In 1921 they contributed a modified Babcock method, which was named the American Association test and later known as the Normal Butyl Alcohol test. This test was recommended as a result of numerous favorable comparisons with the official ether-extraction method and was adopted by some experiment stations and commercial plants. Hunziker (1927) recommends the modified Babcock or ether-extraction methods, while McKay and Larsen (1922) favor the American Association test. The lack of uniformity of results in estimating fat by the different methods indicated that further research was necessary to determine which method could be relied upon.

Petersen observed that when powdered buttermilk was extracted thoroly with alcohol and ether, large quantities of phospholipoids were removed. A review of the literature substantiated these findings. Dornic and Daire (1910) state that buttermilk contains a higher percentage of lecithin than any other milk product, with the possible exception of cream. As a result of this preliminary work, experimental work was initiated to determine the status of the problem.

The results obtained by Thurston and Petersen (1928) and later confirmed by Chapman (1928) showed that the Roese-Gottlieb, the Mojonnier (a commercial adaptation of the Roese-Gottlieb method), and the normal butyl alcohol methods do not give an accurate estimate of the true fat content of buttermilk. This discrepancy was shown to be due to the fact that buttermilk contains relatively large amounts of ether- and alcohol-soluble phospholipoids of which lecithin and cephalin are the principal constituents.

Having definitely established the status of the problem, it became evident that a test was needed whereby the true fat content of buttermilk could be accurately estimated. The researches here reported have revealed such a method, which employs alkaline reagents and the Babcock apparatus.

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[1] Patent applied for.

REVIEW OF THE LITERATURE

The use of alkaline reagents is not a new discovery. Recently Overman and Garret (1928) employed an alkaline solution to estimate the fat content of ice cream. Between 1904 and 1909, considerable discussion for and against the use of alkaline reagents is evident in German literature. The literature is too voluminous for a comprehensive review. It will suffice to mention a few of the first papers dealing with alkaline reagents and their application to the estimation of butterfat in dairy products. Those interested in a summary of the earlier literature are referred to a paper by Windisch (1909).

Owing to patented formulas and trade names, little information can be obtained relative to the composition of the first alkaline reagents made by the German chemists. However, Sichler (1904) was granted four patents on alkaline solutions to which the term "sinacid" was applied. The original "sinacid" reagents consisted of two salt compounds. One was tri-sodium phosphate; the other consisted of tri-sodium citrate and ammonium tri-borate. Amyl or isobutyl alcohol was added separately when making the test. This formula was later modified several times.

Gerber's (1906) "sal" method consisted of a sodium tartrate solution made alkaline with sodium hydroxide plus sodium chloride. The literature reveals considerable contradictory evidence as to the accuracy of Gerber's "sal" and Sichler's "sinacid" methods of estimating the fat content of dairy products as compared to the Roese-Gottlieb method. Two investigators, du Roi and Kohler (1904), showed that with cream the Sichler test checked very closely with the Roese-Gottlieb test, but was a trifle lower than the Gerber "sal" method. They also found the Sichler test to check with the Gerber method on milk testing 3.3 to 3.6 per cent, but the Sichler to be high for milks above 3.3 per cent and low for those below 2.3 per cent fat. For buttermilk, the Sichler test was lower than the Gerber, while for skimmilk the Sichler gave no reading when the Gerber was 0.1 per cent or less.

Gordon (1904) states that for testing buttermilk, skimmilk, cream, whole milk, and cheese by the Sichler "sinacid" method, the test bottles should be heated on a water bath at 65-90° C. He observed that when the test was completed, a dark gummy smudge settled on the bottom of the test bottle. According to his observations, if the test bottles were heated for two hours the fat would separate without centrifuging.

Apparently the interest in testing dairy products with alkaline reagents moderated considerably between 1905 and 1920, owing perhaps to the universal adoption of the Babcock test. However, Höyberg (1921) formulated a new reagent, which he patented, for estimating fat. His approximate formula contained 50-70 grams of sodium hydroxide and 70-130 grams of potassium sodium tartrate per liter. A different mixture of these salts was required for milk and for cream. Orla-Jensen (1923) modified the Höyberg reagent so that the same alkaline solution and mixture of alcohols could be used for milk and cream. He compared this modified reagent with the Roese-Gottlieb and Gerber methods on milk and on cream and found close agreement with Roese-Gottlieb; the Gerber method gave slightly higher results. Orla-Jensen believed that the modified Höyberg method would be universally adopted because of its accuracy and ease and simplicity of operation in that no centrifuge is required.

The Höyberg method was further improved by Spur (1926) who combined the solutions into one reagent, consisting of a mixture of higher alcohols in 4.5 per cent sodium hydroxide. Later (1926) he reduced the alkalinity of the reagent and also reduced the temperature of the water bath to 50° C. This modified Höyberg method checked to the accuracy of 0.1 per cent for milk and 0.5 per cent for cream as compared to the Gerber method. For milk containing less than 0.5 per cent fat and for cheese, a different alkaline reagent and the centrifuge are recommended. Van Woerden (1928) states that the Höyberg method is efficient and accurate and gives an average value only slightly higher than the Gerber, the difference on milk being generally less than 0.05 per cent.

Magliano and Porzio (1927) reported unsatisfactory results with the Höyberg method, and they devised what is essentially a modification. Their alkaline solution is Fehlings B, consisting of 60 grams sodium hydroxide and 173 grams potassium sodium tartrate and the volume made up to 500 cc. with distilled water. The alcohol mixture consists of 45 parts methyl and 55 parts isobutyl alcohol. To estimate fat in milk, the test is manipulated as follows: 10 cc. of milk, 3 cc. of the alkaline reagent, and one cc. of the alcohol mixture are added to a Gerber test bottle and the contents well mixed. The test bottles are next placed in a water bath at 82° C. for about five minutes and are shaken several times during this interval. When the contents of the bottle have taken on an orange color and a layer of fat has separated on the surface, the percentage of fat is read directly after standing three to five minutes. The authors submit data on 56 samples of milk and, as compared to the Gerber method, the results check to within plus or minus 0.07 to 0.1 per cent.

Kreis and Studinger (1927) describe the Neusal method for estimating fat in milk and cream. The alkaline solution consists of sodium citrate and sodium salicylate. Evidently this method is not standardized, because the authors recommend the addition of isobutyl alcohol until the variations, as compared to the Gerber method, are less than 0.05 per cent.

The most recent alkaline method is the one devised for ice cream by Overman and Garret (1928). Their procedure is given in detail in another section.

The review of literature revealed that the principal reason for the large amount of research with alkaline reagents was an endeavor to develop a method that would dispense with the use of acids. No differentiation was made between true fat and the phospholipoid content of dairy products. In fact, the problem of testing buttermilk was not considered.

EXPERIMENTAL

Preliminary experimental work indicated that the alkaline reagents, specified for ice cream by Overman and Garret (1928) and known as the Garret-Overman method, do not include lecithin with the fat in testing buttermilk, using the Babcock equipment. This reagent is composed of 200 grams of tri-sodium phosphate and 200 grams of sodium salicylate made up to one liter with a mixture of three volumes of ammonium hydroxide and seven volumes of water. The procedure used consisted of measuring 9 grams of buttermilk into a Babcock skimmilk test bottle and adding 0.8 cc. of normal butyl alcohol. The contents were mixed well and 9 cc. of the alkaline reagent was added. The test bottles were next placed in a water bath at 71-82° C. for about ten minutes and shaken several times during the heating process. The rest of the procedure was the same as for the regular Babcock method.

This method gave clear fat columns that could be easily read and the duplicates checked. Lecithin added to the extent of 0.3 per cent did not increase the test of buttermilk of known fat content. However, the alkaline solution has several disadvantages. The tri-sodium phosphate crystallizes on cooling, which necessitates heating the reagent before using. The presence of ammonia makes it objectionable to handle, and experience indicated that the solution deteriorates on standing.

A number of modifications of the Garret-Overman formula were tried by varying the concentration of the salts and the amount of normal butyl alcohol, but the results did not check with those obtained with the recommended reagent. One modification whereby dry tri-sodium phosphate was added to dry test bottles, followed by the buttermilk and the other reagents, gave results comparable with the standard formula and obviated the difficulty of crystallization.

The favorable results obtained with the Garret-Overman reagent encouraged further research, which led to the development of a practical test for buttermilk, using alkaline reagents and the Babcock apparatus. Space will not permit publication in detail of the formulas of forty-six different combinations tried experimentally in this laboratory. Several combinations were used that gave excellent results on buttermilk, but the reagent selected showed possibilities of application to other dairy products. This reagent consists of 110 grams of sodium carbonate and 200 grams of sodium salicylate dissolved in water and the volume made up to 1,000 cc. To this solution is added 30 cc. of 50 per cent sodium hydroxide and 100 cc. of normal butyl alcohol. The name given to this solution is "The Minnesota Babcock Test Reagent."

The method used for testing buttermilk employing this reagent is as follows:

1. Nine grams of buttermilk are placed in a skimmilk test bottle.
2. Ten cc. of the Minnesota reagent is added and the contents of the bottle are well mixed.
3. The test bottles are placed in a water bath at 71-82° C. for six to seven minutes, and shaken several times during this interval.
4. The bottles are centrifuged for five minutes at a speed of 800 revolutions per minute in an 18 inch centrifuge.
5. Warm water is added to the base of the neck of the test bottles and they are centrifuged for two minutes.
6. Sufficient warm water is added to bring the fat into the graduated neck of the test bottles and the centrifuge is operated for another minute.
7. The test bottles are placed in a water bath at 57-60° C. for five minutes and the fat reading taken is multiplied by 2 because a 9-gram sample of buttermilk is used.

This method gave excellent results. The contents of the test bottle after completing a buttermilk fat determination were only slightly opaque, indicating that the solids-not-fat were highly dispersed in the alkaline solution.

Having developed a method that showed promise of giving a true estimate of the fat content in buttermilk, it became evident that further research was necessary to determine its accuracy and applicability under practical laboratory conditions.

Natural buttermilk was used. The advisability of using synthetic milk was considered but not adopted, owing to the impossibility of duplicating the physical properties of natural buttermilk. Additions of fat and of lecithin were made by weighing definite amounts into a known weight of buttermilk. All weighings were made on an analytical balance. It is obviously wrong to make additions of fat or lecithin to a given volume of buttermilk and assume such additions to be on a percentage basis.

The lecithin used in this experimental work was originally prepared from dried egg yolks according to Maclean's (1918) method, and was granular and light yellow in color. However, the purity of lecithin prepared by this method is questionable. Owing to the solubility of fat in acetone, which is a phospholipoid precipitant, it is reasonable to expect that some fat would be enclosed within the lecithin particles during the purification process. Fortunately the literature revealed a method whereby fat-free lecithin could be prepared.

Gies (1912) and his associates, in their diffusion studies, found that fat could be separated from lecithin by dialysis. According to this method lecithin-fat mixtures are dissolved in ether and the contents poured into a thin rubber container surrounded by ether. The fat diffuses through, leaving the lecithin behind.

The lecithin used in the experiments herein reported was purified according to this method. Dialysis was continued for four days. The diffusate were then removed and a fresh supply of ether added and dialysis continued for another two days. The amount of fat in the diffusate was not determined quantitatively, but upon evaporation of the ether a residue of fat-like material was obtained. This residue, when dissolved in ether and acetone added in excess, did not yield a precipitate, indicating that it was an ether- and acetone-soluble substance, probably mostly fat. The nitrogen and phosphorus content of the lecithin, 1.925 and 4.220 per cent, respectively, is higher than figures previously reported in the literature. This is considered sufficient evidence that the lecithin used in this experimental work was as pure as it is possible to obtain with present methods.

The butterfat used was rendered and clarified on a water bath funnel, filtered and subjected to high centrifugal force. The filtering and centrifuging processes were repeated three times. A portion of the purified butterfat was weighed into an aluminum evaporating dish, placed in a vacuum oven at 135° C. for five minutes, cooled, and on reweighing showed no loss in weight, indicating that the butterfat was moisture-free.

The data reported in the following section are a summary of experiments conducted to determine the accuracy of the Minnesota Babcock test reagent in comparison with the other methods of estimating fat in buttermilk.

EFFECT OF ADDING LECITHIN TO BUTTERMILK ON FAT DETERMINATIONS BY VARIOUS METHODS

The results recorded in Table I substantiate the findings of Thurston and Petersen (1928) and Chapman (1928) in that the Mojonnier and normal butyl alcohol methods for estimating fat include lecithin. However, results obtained with the Babcock tests are at variance with those obtained by Chapman. He was able to recover an average of 71 per cent of the lecithin added, while in the experiments here reported only slight increases in the fat tests were obtained by the Babcock method that could be attributed to added lecithin.

When testing buttermilk to which lecithin was added, by the Babcock method, it was observed that partially hydrolyzed material, presumably lecithin, aggregated at the base of the neck of the test bottles. This obstruction probably prevented the rising of fat globules into the neck of the test bottle, and accounts for the low results obtained with the Babcock method. It was found possible to force some of the hydrolyzed material into the small neck of the test bottle by increasing the speed of the centrifuge.

TABLE I

EFFECT OF ADDING LECITHIN TO BUTTERMILK ON FAT DETERMINATIONS BY VARIOUS METHODS

Sample No.	Added lecithin per cent	Methods used and fat percentages									
		Mojonnier		Babcock		Normal butyl alcohol		Garret-Overman reagents		Minnesota Babcock test reagent	
A 1	0.0	0.5601	0.5623	0.01	0.01	0.48	0.48	0.32	0.28		
A 2	0.1	0.6863	0.6488	0.01	0.01	0.52	0.72	0.30	0.30		
A 3	0.2	0.7557	0.7434	0.03	0.02	0.60	0.56	0.30	0.28		
A 4	0.3	0.8389	0.8445	0.06	0.14	0.64	0.66	0.28	0.26		
B 1	0.0	0.5930	0.5920	0.05	0.05	0.42	0.40	0.30	0.30	0.30	0.30
B 2	0.1	0.6740	0.6760	0.04	0.05	0.44	0.48	0.31	0.30	0.32	0.30
B 3	0.2	0.7470	0.7420	0.10	0.08	...	0.52	0.26	0.29	0.30	0.29
B 4	0.3	0.8540	0.8310	0.08	0.14	0.78	0.66	0.28	0.30	0.30	0.30
C 1	0.0	0.5500	0.5450	0.08	0.07	0.54	0.56	0.28	0.30	0.32	0.30
C 2	0.1032	0.6512	0.6449	0.08	0.10	0.52	0.57	0.29	0.24	0.28	0.30
C 3	0.2042	0.7503	0.7360	0.22	0.20	0.65	0.68	0.24	0.26	0.29	0.28
C 4	0.3074	0.8419	0.8500	0.18	0.18	0.60	0.62	0.30	0.29	0.30	0.27
D 1	0.0	0.5995	0.5994	0.16	0.14	0.60	0.62	...	...	0.52	0.54
D 2	0.1066	0.6855	0.7182	0.20	0.22	0.70	0.71	...	...	0.54	0.54
D 3	0.2027	0.8086	0.8092	0.40	0.31	0.74	0.70	...	...	0.50	0.48

In no case did added lecithin increase the fat tests when the Minnesota and the Garret-Overman methods were used. This is considered conclusive evidence that these reagents, using the Babcock apparatus, do not include lecithin in estimating the fat content of buttermilk.

EFFECT OF ADDING FAT TO BUTTERMILK ON FAT DETERMINATIONS BY VARIOUS METHODS

The results obtained by the addition of lecithin to buttermilk showed that the Minnesota and the Garret-Overman methods do not estimate lecithin. However, the question arose as to whether these reagents would remove all the fat. Therefore it was thought advisable to determine the effect of added fat, and in Table II are recorded the results.

TABLE II

Effect of Adding Fat to Buttermilk on Fat Determinations by Various Methods

Sample No.	Added fat per cent	Methods used and fat percentages									
		Mojonnier		Babcock		Normal butyl alcohol		Garret-Overman reagents		Minnesota Babcock test reagent	
E 1......	0.0	0.5601	0.5623	0.01	0.01	0.48	0.48	0.32	0.28		
E 5......	0.1	0.6714	0.7025	0.08	0.07	0.65	0.68	0.40	0.40		
E 6......	0.2	0.7350	0.7344	0.14	0.15	0.74	0.70	0.50	0.50		
E 7......	0.3	0.8420	0.8260	0.28	0.28	0.84	0.83	0.60	0.64		
F 1......	0.0	0.5930	0.5920	0.05	0.05	0.40	0.42	0.30	0.30	0.30	0.30
F 2*.....	0.1	.....	.....	...	...	...	...	...	...	...	...
F 3......	0.2	0.7880	0.7710	0.18	0.22	0.76	0.64	...	0.48	0.50	0.50
F 4......	0.3	0.8260	0.8450	0.28	0.28	0.76	0.72	0.60	0.60	0.60	0.58
G 1......	0.0	0.5500	0.5450	0.08	0.07	0.54	0.56	0.28	0.30	0.32	0.30
G 2......	0.1025	0.6250	0.6270	0.06	0.06	0.58	0.60	0.28	0.29	0.39	0.39
G 3......	0.2043	0.7283	0.7369	0.10	0.07	0.64	0.64	0.36	0.44	0.50	0.49
G 4*.....	0.3021	.....	.....	...	...	...	...	...	...	...	...

* This sample was accidentally lost.

It is evident that added fat was not quantitatively recovered, tho the Minnesota and the Garret-Overman methods gave the best results. The failure of the Mojonnier method to recover the added fat was difficult to explain, but on emptying the flasks containing the buttermilk a layer of fat was observed on the inside of the container. This source of error and the fact that the Mojonnier fat determinations were made after all the other tests were completed, undoubtedly accounts for the incomplete recovery of fat. With the exception of buttermilks Nos. G 1 and G 2, the normal butyl alcohol tests are increased with each addition of butterfat, but the results with the Babcock tests show little uniformity.

EFFECT OF ADDITION OF BOTH LECITHIN AND FAT TO BUTTERMILK ON FAT DETERMINATIONS BY VARIOUS METHODS

Lecithin is known to be a good emulsifier and if present in sufficient quantities in buttermilk would act as a fat stabilizer. This being true, a relatively high lecithin content in buttermilk would change the surface and interfacial tension relationships existing between the fat and the lecithin phase. Because these physical properties are important in testing buttermilk, it was thought advisable to prepare several buttermilks in which the fat or the lecithin or both are varied in concentration and note particularly the recovery of fat by the Minnesota Babcock method in the presence of relatively large amounts of lecithin.

TABLE III

EFFECT OF ADDING BOTH LECITHIN AND FAT TO BUTTERMILK ON FAT DETERMINATIONS BY VARIOUS METHODS

Sample No.	Added fat, per cent	Added lecithin, per cent	Methods used and fat precentages							
			Mojonnier		Babcock		Normal butyl alcohol		Minnesota Babcock test reagent	
H 1	0.0	0.0	0.5879	0.5797	0.12	0.14	0.60	0.60	0.44	0.46
H 2	0.2103	0.1031	0.8983	0.8973	...	0.30	0.64	0.64	0.63	0.65
H 3	0.2065	0.2056	0.9805	0.9688	0.28	0.30	0.76	0.76	0.62	0.62
H 4	0.1054	0.2033	0.8898	0.8854	0.18	0.20	0.68	0.70	0.56	0.56

The results are summarized in Table III. It is evident that the addition of lecithin did not inhibit the complete recovery of fat. Therefore it is safe to assume from these results that an abnormally high phospholipoid content in buttermilk will not interfere with the estimation of fat by the Minnesota method.

QUANTITATIVE RECOVERY OF LECITHIN AND FAT BY THE MOJONNIER METHOD FOR DETERMINING FAT

Contrary to the results obtained in this laboratory by Thurston and Petersen (1928), Chapman (1928) showed that lecithin added to buttermilk was not recovered quantitatively by the Mojonnier method. Because of these contradictory results, we are submitting additional evidence to clarify the situation.

TABLE IV

QUANTITATIVE RECOVERY OF LECITHIN AND FAT BY THE MOJONNIER METHOD FOR DETERMINING FAT

Sample No.	Added fat, per cent	Added lecithin, per cent	Ether extract by Mojonnier method, per cent		Average, per cent	Recovery of fat and lecithin, per cent
I 1	0.0	0.0	0.5879	0.5797	0.5838	.....
I 2	0.2103	0.1031	0.8983	0.8973	0.8978	100.00
I 3	0.2065	0.2056	0.9805	0.9688	0.9746	97.86
I 4	0.1054	0.2033	0.8898	0.8854	0.8876	99.40
J 1	0.0	0.0	0.5995	0.5994	0.5994	.....
J 2	0.0	0.1066	0.6855	0.7182	0.7018	99.40
J 3	0.0	0.2027	0.8086	0.8092	0.8089	100.80

While the recovery of fat and of lecithin, as shown in Table IV, is not exactly within the realm of quantitative accuracy, yet all sources of error considered, the figures show that pure lecithin can be recovered quantitatively by the Mojonnier method. These data further emphasize the inaccuracies incurred when the fat content of buttermilk is estimated by the Roese-Gottlieb and the Mojonnier methods.

RELATION OF THE FAT CONTENT OF THE CREAM TO THE PHOSPHOLIPOID CONTENT OF THE BUTTERMILK

We have shown that the Mojonnier method of fat extraction includes lecithin. Then it can be assumed that the other alcohol- and ether-soluble phospholipoids are also extracted. We have further shown that the Minnesota method does not estimate lecithin. With these facts at hand we can calculate the phospholipoid content of buttermilk as the difference between the fat determinations according to the Mojonnier and the Minnesota tests.

TABLE V

Fat Percentage of the Cream in Relation to the Phospholipoid Content of the Buttermilk

Measured by the difference between the fat determination according to the Mojonnier and the Minnesota methods

Churning No.	Fat content of cream, per cent	Fat in buttermilk				Calculated phospholipoids, per cent
		Mojonnier, per cent		Minn.-Babcock test reagent, per cent		
A 1	38.5	1.5020	1.5152	1.00	1.00	0.5086
A 2	21.0	1.2017	1.2382	0.90	0.90	0.3199
B 1	35.5	1.9830	1.9522	1.50	1.55*	0.4426
B 2	18.5	0.6593	0.6466	0.40	0.40	0.2529
C 1	38.5	1.7985	1.8110	1.35	1.35*	0.4547
C 2	19.0	0.7637	0.7304	0.44	0.44	0.3070
D 1	34.0	1.8900	1.8780	1.55	1.55*	0.3340
D 2	19.5	1.2439	1.2429	1.10	1.05	0.1684
E 1	39.5	3.0339	3.0292	2.50	2.50*	0.5315
E 2	19.0	1.3531	1.3760	1.10	1.10	0.2645
F 1	38.5	3.2650	3.2921	2.90	2.85*	0.4035
F 2	20.0	0.9347	0.9503	0.72	0.74	0.2125
G 1	36.0	2.4268	2.4319	2.10	2.15*	0.3043
G 2	18.5	0.9652	0.9548	0.70	0.71	0.2550

* Fat estimated in whole-milk test bottle, and a small amount of glymol placed on the surface of the fat to remove the meniscus.

Dornic and Daire (1910) state that lecithin is concentrated on the surface of the fat globules and is detached during the churning process. Palmer and Samuelson's (1924) work supports this explanation. If this is true, buttermilk from high testing cream should contain relatively larger amounts of phospholipoids.

To study the relative phospholipoid content of buttermilk from creams of high and of low fat content, a series of seven comparisons was made, a total of fourteen churnings. In each case a cream of high fat content was obtained. A part of it was churned and the remainder was standardized with skimmilk. Five pounds of cream was churned in Dazey churns and temperatures were carefully controlled. The figures in Table V show that the calculated phospholipoid content is higher for buttermilk from creams of high fat content. With the exception of churnings 13 and 14 the difference as compared to buttermilk from low-testing cream is more than 0.1 per cent. These figures are only approximate, because the limit of accuracy in reading a Babcock whole-milk test bottle is 0.1 per cent. With more finely calibrated test bottles, our method of calculations should give a true estimate of the phospholipoid content of buttermilk.

PURITY OF FAT AS EXTRACTED BY THE MINNESOTA METHOD

The experimental evidence in this paper indicates that the Minnesota method is free from the objectionable features of the normal butyl alcohol and the Mojonnier methods in that the alcohol- and ether-soluble phospholipoids are not extracted and estimated as true fat. However, the question was raised as to the purity of the fat estimated by the Minnesota method. This was in part proved by the results recorded in Table II where added fat was recovered quantitatively, but did not preclude the possibility of the fat being contaminated with alcohol from the alkaline reagent, an observation reported by earlier workers (Sichler, 1904).

We proceeded to determine the purity of the fat by estimating the fat content of buttermilk with a type of skimmilk test bottle having a removable neck (known in the trade as "Russian"). A 9-gram sample of buttermilk was used. The fat in the removable neck was washed with ether into a weighed Mojonnier evaporating dish. The dish was placed in the Mojonnier vacuum oven at 135° C. for five minutes, cooled and weighed. From the net weight of the dried residue and the weight of the buttermilk sample, the fat percentages were recalculated and compared with the original volumetric readings. It is evident from the results recorded in Table VI that the fat was not contaminated with any appreciable quantity of foreign volatile material.

TABLE VI

PURITY OF FAT AS EXTRACTED BY THE MINNESOTA METHOD
Determined by drying in a vacuum oven

Sample No.	Fat content as read from test bottle	Recalculated fat content*
	per cent	per cent
1	0.40	0.394
2	0.39	0.375
3	0.38	0.365
4	0.34	0.293

* As determined from weight of dried fat residue and weight of buttermilk sample.

SOME FUNDAMENTAL CONSIDERATIONS OF THE MINNESOTA BABCOCK TEST REAGENT

The separation of the fat from the other ingredients is affected by a dispersion of the non-fatty materials of milk and a change in the interfacial tension between the fat particles and the solution. The interfacial tension is so affected by the alcohol that the fat particles rapidly coalesce and separate as a clear liquid layer. The alcohols are readily soluble in the alkaline solution, where they remain and do not contaminate the supernatant fat.

The alkaline solution disperses the milk solids-not-fat, including the phospholipoids. The soluble alkaline salts act as buffers, which eliminates the danger of fat saponification. Subjecting samples of buttermilk mixed with the reagent to a temperature of 77-82° C. for thirty minutes did not affect the fat reading. A one per cent aqueous lecithin emulsion was exposed to the action of the reagent for five minutes at 82° C. and, when acetone was added, a precipitate of apparently normal lecithin was obtained. The presence of choline in the molecule, which is strongly alkaline, probably accounts for the stability of lecithin toward alkalies, whereas lactose is readily oxidized because of the instability of sugars in alkaline solutions. Furthermore, the soluble salts in the reagent do not crystallize on standing at room temperature, 21° C. At lower temperatures crystallization takes place and it becomes necessary to heat the reagent slightly before using. Creamery operators have used this reagent for the last five months for testing buttermilk and report excellent results.

SUMMARY

1. Further evidence is presented to show that the phospholipoids are a factor in estimating the fat content of buttermilk.

2. A method is described for determining the true fat content of buttermilk.

3. Preliminary work indicates that the Minnesota Babcock test reagent may be used to estimate the fat content of other dairy products, including ice cream and condensed milk. However, more extended studies are necessary before definite recommendations can be made.

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University of Minnesota
Agricultural Experiment Station

Some of the Factors Influencing the Growth of Molds in Butter

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CONTENTS

Page

Introduction 5

Review of literature 6

Factors influencing the growth of molds on butter 7

- Food supply 7
- Moisture 11
- Atmosphere 14
- Temperature 15
- Miscellaneous chemical and physical environment 16
- Species of molds isolated from butter 20

Experimental 21

- Purpose of study 21
- Method of procedure 21
  - Species of molds used in experiments 22
  - Methods employed in experiments 22
  - Manner of recording results 22

Experimental results 23

- A. Food supply 23
  - 1. Fats and related substances 23
    - a. Fresh butterfat 23
    - b. Old butterfat 24
    - c. Butterfat from washed cream 25
    - d. Butterfat washed with alcohol 26
    - e. Fresh butterfat plus water 27
    - f. Old butterfat plus water 28
    - g. Alcohol-extracted butterfat plus water 29
    - h. One-half per cent aqueous emulsion of milk lecithin 30
    - i. One-half per cent aqueous emulsion of milk lecithin in 1.5 per cent washed agar 30
    - j. One per cent glycerol in 1.5 per cent washed agar 31
    - k. One per cent butyric acid in 1.5 per cent washed agar 32
    - l. One per cent palmitic acid in 1.5 per cent washed agar 32
    - m. One per cent stearic acid in 1.5 per cent washed agar 33
    - n. One per cent oleic acid in 1.5 per cent washed agar 34
  - 2. Proteins and related substances 34
    - a. One per cent aqueous solution of peptone 34
    - b. Curd portion of butter 35
    - c. Dialyzed curd from butter 36
    - d. Washings from cream 36
  - 3. Carbohydrates and related substances 37
    - a. One per cent aqueous solution of lactose 37
    - b. One per cent aqueous solution of lactose in 1.5 per cent washed agar 38
    - c. One per cent lactic acid in 1.5 per cent washed agar 38
    - d. Diffusate from curd of butter 39
  - 4. Mineral constituents 39
    - a. Milk ash in 0.75 per cent aqueous solution 39
    - b. Milk ash in 0.75 per cent aqueous solution neutralized with hydrochloric acid 40

Page
5. Combinations of various foodstuffs ... 41
  a. Emulsion of butterfat, milk lecithin, and water ... 41
  b. Butterfat plus dry milk ash ... 41
  c. Mixture of butterfat, milk ash, and water ... 42
  d. Aqueous solution of lactose and peptone ... 43
  e. Mixture of lactose and peptone in 1.5 per cent washed agar 43
  f. Sterile, unsalted butter ... 44
B. Moisture ... 45
  1. Moisture in substrate ... 45
  2. Moisture in atmosphere ... 45
    a. Effect of humidity on growth of molds on unsalted butter .. 45
    b. Effect of humidity on the growth of molds on unsalted butter churned from inoculated cream ... 47
C. Temperature ... 47
  1. Growth on whey broth ... 48
  2. Growth on whey agar slants ... 48
  3. Growth in sweet buttermilk ... 50
  4. Growth on sterile butter ... 50
  5. Growth on butter made from inoculated cream ... 52
D. Atmosphere ... 52
  1. Ordinary air supply ... 54
  2. Reduced air supply—partial vacuum ... 54
  3. Partial removal of carbon dioxide ... 54
  4. Removal of oxygen ... 55
E. Miscellaneous chemical and physical factors ... 56
  1. Salt content ... 56
    a. Whey broth plus salt ... 56
    b. Whey agar plus salt ... 56
    c. Sterile, sweet buttermilk plus salt ... 58
    d. Sterile, sour buttermilk plus salt ... 58
    e. Sterile butter plus salt ... 60
    f. Sterile butter plus salt ... 62
    g. Butter made from inoculated cream plus salt ... 63
Discussion of results ... 64
  Food supply ... 64
  Moisture ... 70
  Temperature ... 72
  Atmosphere ... 72
  Salt ... 73
  Species of molds ... 74
Summary ... 75
Bibliography ... 77

ILLUSTRATIONS

Plate 1. Comparative growth of test cultures on one per cent lactose in 1.5 per cent washed agar and on one per cent lactose + one per cent peptone in 1.5 per cent washed agar ... 87
Plate 2. Penetration of mycelium into substrate ... 88
Plate 3. Typical appearance of growth of test cultures on unsalted butter 89
Plate. 4. Effect of salt concentration upon the growth of *Hormodendrum cladosporioides* in butter ... 90

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SOME OF THE FACTORS INFLUENCING THE GROWTH OF MOLDS IN BUTTER[1]

HAROLD MACY

INTRODUCTION

The market value of butter is determined, in a large measure, by flavor and aroma, but the general appearance and physical structure also have considerable influence upon a critical and discriminating buyer.

One of the most disturbing defects of market butter is due to the growth of molds, which produce discolored areas on the surface of the butter, wrapper, or packing, often sufficiently serious to cause rejection by the dealer. On the other hand, the mold growth may be such that there are no marked, visible signs of molding to mar the appearance of the butter, but quite enough to bring about decided, deleterious changes in the flavor and aroma. The discoloration due to the growth of molds is always a serious matter, but when the flavor and aroma may be affected simultaneously, or even independently, as they are by the development of certain molds, the situation assumes very serious proportions. As a rule the market has been thinking of the molding of butter principally as a defect in appearance, because this is the most striking manifestation of the development of these microörganisms.

Generally, moldy butter occurs as an isolated case, altho at times an outbreak of moldiness from certain creameries may assume the proportions of an epidemic. When such a situation arises, losses to the creameries are often heavy, involving hundreds or thousands of dollars, quite sufficient to cause a minor financial crisis for large creameries and a major crisis for smaller establishments. In recent years, moldy butter has attracted much more attention than it did formerly. The reason for this is not entirely clear, altho changes in manufacturing methods and a more discriminating market may have had a part in this increased interest.

The appearance of mold has been more frequent in unsalted butter, and occurs most commonly during the early spring and summer months. However, isolated cases may occur at any season of the year and in various grades of butter and margarine.

The mold problem is really serious for the creamery industry, considering the damage done by the mold in producing the typical surface discoloration and deterioration of the product. A number of investigators have studied some of the factors that may influence the growth of mold in butter, but some factors have not been studied carefully, and must be understood clearly before the industry controls the situation. For instance, it has been generally agreed that salt has a preservative action in butter and tends to prevent moldiness. Nevertheless, many cases of mold occur in highly salted butter. The problem is not simple, nor will it be easy to solve. So many factors may influence the growth of molds in butter that each must be studied thoroly before a proper evaluation can be made for individual species and mixtures of species that may occur in a given lot of butter. The relationship of these factors, one to the other, must be established before the problem can be approached with a reasonable degree of assurance that it can be solved and control exercised.

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[1] The material in this bulletin was submitted to the Graduate Faculty of the Iowa State College in partial fulfillment of the requirements for the degree of Doctor of Philosophy, granted June, 1929.

The studies reported here were undertaken in an attempt to provide data from which future research may be directed toward a more complete solution of the problem.

REVIEW OF LITERATURE

There is no indication in the literature as to the original observation of the molding of butter. Undoubtedly, mold growth occurred on butter made under primitive conditions and stored where there was every opportunity for growth. For many years articles on dairying have referred to the appearance of discolored areas on butter, but before mycological laboratory methods were perfected little definite information was available. Saccardo (111) in 1886 stated that *Oospora ruberrima* had been reported by Trabut as occurring on butter in Algiers. Duclaux (34) in 1886 mentioned the fact that molds were found in butter. In 1892, Siedel (124) found that granular butter, stored for several months in brine, changed in flavor and developed roquefort, turnipy, or beet flavors, which he attributed to molds. McWeeney (80) in 1894 described and illustrated a fungus, causing dark brown spots on butter exhibited at Cambridge, that he considered to be like *Dematium pullulans* DeBary, but which was identified as *Cladosporium herbarum* Link. Reference to mold in butter was made from Sweden anonymously (4) and by Wågepetersen (141). Shaw (123) reported that several samples of butter in Portland, Oregon, developed bluish-black isolated spots on the surface, which eventually became covered with the growth of a fungus identified as *Stemphylium butyri*. He also stated that a similar case had been noted in North Carolina. In an extended report upon experimental exports of unsalted butter to the London market, published by the United States Department of Agriculture, Alvord (2) stated that results were unsatisfactory because a portion of the butter became moldy. In a monograph that has been quoted widely, Gripenberg (53) discussed the investigations carried on during the years 1896-1898 in Finland to determine the causes of moldy butter. The molding of butter had become a serious problem for the exporters of Finnish butter and demanded some study. During the last 30 years there have been increasing numbers of references to the appearance of mold in butter, and results of research upon sources, species of molds, factors influencing growth, chemical activity, and methods for control have been published. Many of these will be discussed.

FACTORS INFLUENCING THE GROWTH OF MOLDS ON BUTTER

Many factors may be considered as affecting the growth of molds, among which the food supply, moisture, atmospheric conditions, temperature, and miscellaneous physical and chemical environment are the most noteworthy. Furthermore, the species of mold undoubtedly is an important factor. These factors will be considered separately.

Food Supply

Butter carries a variety of food elements—fats, proteins, carbohydrates, and mineral salts—which should provide nutriment for the molds that may be present.

1. **Fats and related substances.**—As fat is the principal constituent of butter, it is well to consider the part which fat may play in the nutrition of some of the common fungi. In an investigation of the use of fats by certain fungi, Schmidt (117) found that when various oils were added to a mineral solution, the molds grew and utilized, especially, the neutral fats. The decomposition of a glyceride was considered as beginning with a splitting into glycerol and the fatty acids, which in turn might be attacked. If the oil covered the surface of the nutrient solution, the molds were shut off from oxygen and did not grow. Duclaux (35) melted a sample of butter and decanted a portion of the fat. The remainder of the sample was emulsified and inoculated with a species of Penicillium. Changes took place in the fats and there were variations in the proportion of fatty acids released. Butyrin was saponified more easily by the culture than caproin, but both were found to be more readily attacked than the other glycerides. Later, Duclaux (36) found that if an oil was impure and carried a substance that imbibed water, the surface of the substrate might be covered after a few days by an abundant vegetation in which *Penicillium glaucum* predominated. Water played an important rôle in this growth of mold especially as it might carry various nutrients and furnish moisture for germination. In a study of rancidity of butter, Hanus (56) reported that the glycerides of the saturated fatty acids

were decomposed by molds but that those of the unsaturated acids were not. He pointed out later (57) that the molds first attacked the lactose and proteins and later decomposed the fats. Eichholz (39) (40) made the statement that microörganisms could not grow in pure butterfat but that *Penicillium glaucum* developed especially well and caused an intense roquefort flavor in butter rich in casein. Crampton (25) (26) concluded from his experiments with moldy oleomargarine that where nitrogenous or other non-fatty material afforded a nutritive medium for the growth of molds, edible fats could be hydrolyzed so that fatty acids and glycerol were liberated. Laxa (72) found that molds brought about an important decomposition of butterfat; but that the splitting of all glycerides did not take place in the same degree. The glycerides of the insoluble fatty acids that have higher molecular weights were found to be more easily hydrolyzed by the molds than those of lower molecular weights, and the toxicity of the freed, soluble fatty acids increased with the increasing molecular magnitude. Schreiber (118) found that pure fat by itself was not a foodstuff for the microörganisms that he studied, but where other nutrients were available molds were able to split the fat. As a result of his experiments Rahn (99) concluded that the decomposition of fat took place only in the presence of organic nitrogen. Kühl (70) (71) reported that molds isolated from butter were able to attack fat, but that this process took place after the molds had made their original development on the curd of butter. Roussy (109) investigated the value of fatty substances as food for *Phycomyces nitans, Rhizopus nigricans,* and *Sterigmatocystis nigra*, and stated that for these molds fat was just as good food as carbohydrates. His studies (110) were continued with similar results when other species were used. Söhngen (125) found that several molds were capable of producing lipase, which split the fat in butter and margarine. In extensive investigations Spieckermann (126) (127) studied the effect on fats of cultures of *Penicillium glaucum* and other molds. The fats were split in a variety of ways when some nitrogenous compounds were present in the substrate. Batten and Bywaters (9) in experiments with sterile cacao butter, observed that molds would not grow on it at any temperature unless water was present. Colonies did appear on a solidified emulsion of the cacao butter and water (about 30 per cent) after 3 months at room temperature. When small quantities of sterile prune juice agar were mixed with cacao butter, vigorous growth was observed in less than a week. Bywaters (21) also stated that pure fats were very resistant to the attack of fungi, probably because of the lack of nitrogenous and other elements required for growth. As a result of researches on the rancidity of vegetable margarine, Jacobson (62) decided that the influence of molds on absolutely dry cocoanut oil was of no significance, but if only traces of water were present rancidity might occur. Stokoe (129) found that *Penicillium glaucum* when inoculated into pure fats produced little change, but when the fats were emulsified with nutrient media the mold developed within a few days. He (130) stated that the development of rancidity in water-free fats was not due to the activity of microörganisms. The products formed as a result of the action of *Penicillium sp.* were discussed in a later publication by the same author (131). Flieg (49) studied the action of *Aspergillus niger* on a variety of fats in a synthetic medium that encouraged the early growth of the fungus, and found that the different fats were attacked in different ways. After reviewing the literature extensively, Stärkle (128) stated hat the presence of water and nitrogenous substances was necessary for the growth of molds in cocoa fat. Zikes (147) likewise made the statement that pure fats and waxes did not support the growth of fungi and that positive results in the past were probably due to adherent traces of proteins and carbohydrates. In a recent publication, Patil and Hammer (92) reported that butterfat in a purified condition seemed quite resistant to the growth of microörganisms. Strained fat and ghee kept much better than butter or ghee containing added water.

Schmidt (117) found that when a mineral nutrient was provided, oleic and palmitic acids were more or less satisfactory sources of carbon for *Aspergillus niger,* after glycerides were broken down into he component acids and glycerol. According to Bokorny (14) butyric acid may be used as food for molds, but Bitting (11) found that a 0.2 per cent solution retarded the growth of Penicillium, while *Oidium actis* did not develop in more than 0.1 per cent. Crampton (26) found hat *Coniothecium sp.* attacked the fatty acids freed in oleomargarine, with a preference for those of lower molecular weights. Rahn (99) agreed that fungi show a preference for the lower acids. Laxa (72) reported the utilization of volatile fatty acids released in the splitting of butterfat by molds. Spieckermann (126) found that certain molds were able to use fatty acids, especially if they were finely divided. Roussy (110) was able to obtain good growth of several species of mold on oleic, palmitic, and stearic acids when they were used in connection with Raulin's medium. Tausson (132) reported that oleic, stearic, and palmitic acids were utilized by *A. flavus,* altho the saturated acids were more suitable than the oleic acid. Kiesel (66) was of the opinion that fatty acids show considerable toxicity toward *Aspergillus niger,* especially those containing the most carbon. In this respect the molecular structure also appeared to be significant. The differences in toxicity were explained on the basis of the differences in penetrability of the protoplasmic layer of the cell for various substances.

The glycerol released by the splitting of fats could be readily utilized by fungi, according to Burr (19) who found that *Penicillium glaucum* and *Aspergillus niger* would grow in 43 per cent glycerol solutions. Ehrlich (38) demonstrated that *Oidium lactis* utilized glycerol as a food. Roussy (110) came to the conclusion that the several species of molds which he was studying developed much better on fatty acids than on glycerol, with the exception of species of Penicillium and Aspergillus. Glycerol did not serve particularly well as a source of carbon, according to Schmidt (117).

When ivory-nut oil and lecithin were added to a nutrient medium, von Euler (44) found that the growth of *Penicillium glaucum* and *Rhizopus chinensis* was extensive after the medium was irradiated by ultra-violet light.

Apparently, pure fat is not available for direct use by molds; sufficient quantities of water and nutrient substances appear to be necessary before the splitting and utilization of the fat can be accomplished. There is some question as to the action of molds upon the free fatty acids. A difference appears to exist between the value of the different acids, because of their composition, structure, or some other factor. Large quantities might be toxic and small amounts stimulating. Apparently glycerol and lecithin are able to furnish a satisfactory food supply for many molds.

2. **Proteins and related substances.**—The literature abounds with references to experiments undertaken to determine the type of nitrogen compound most useful for various species of mold. They are so extensive that no attempt will be made to review them. As normal butter contains a considerable quantity of rich nitrogenous material in the form of the droplets of buttermilk, it may be assumed that the molds will find a variety of proteins and related compounds sufficient for growth, providing the molds are in such a position that they are able to obtain the substances directly.

The question may arise as to the possibility of molds fixing nitrogen when they are attempting to grow in such a substance as pure butterfat. Dox (32) (33) reported that he found no evidence that *Aspergillus fumigatus* could fix nitrogen. The literature upon the subject of nitrogen fixation has been reviewed very thoroly by Duggar (37) who came to the conclusion that nitrogen fixation could not be established for *Aspergillus niger*, *Penicillium digitatum*, *Penicillium expansum*, and some other forms, while *Phoma betae* showed signs of fixation when growing on mangel and sugar beet decoction with sugar.

As far as the utilization of the protein fraction of butter is concerned, Batten and Bywaters (9), Burr and Wolff (19), Crampton (26), Eichholz (40), and Laxa (73), all expressed the opinion that a high curd content favored the growth of molds in butter. Boekhout and de Vries (12) held that the percentage of curd in itself was not a factor, because the merest traces of curd were sufficient to encourage the growth of mold. This observation seems to be more in accordance with the facts relating to the quantities of nitrogenous material necessary for the development of fungi.

3. **Carbohydrates and mineral salts.**—The value of various carbohydrates and mineral elements or salts as food for molds has been studied by many workers. It would be impractical to present a review of the voluminous literature upon this subject. In connection with studies on butter, it was reported anonymously (5) that lactose was not a good source of food for *Oidium lactis* or *Mucor mucedo*, but was fairly satisfactory for *Penicillium glaucum*. In solutions containing sugar, a marked submerged mycelial development was noted. This observation is of interest in light of the findings presented later. Boekhout and de Vries (12) reported that lactose was not the best type of sugar for *Hormodendrum cladosporioides*. In his studies on the influence of lactose on the decomposition of casein by microörganisms, Laxa (73) found that proteolysis was favored by the presence of lactose. According to Ehrlich (38) *Oidium lactis* was able to utilize lactic acid that might be formed by the hydrolysis of lactose.

The fact that for years the majority of studies on molds have been made upon synthetic media containing a variety of inorganic salts, is evidence that mineral elements are satisfactory and necessary food sources, if they are present in the proper compounds and in the proper quantities. Normal buttermilk carries a variable quantity yet more or less satisfactory variety of most of the inorganic elements essential for the development of many fungi.

As a whole, butter contains a variety of food elements, some of which are readily available for use. Much depends upon the molds being properly oriented so that they are in intimate contact with the most easily utilizable compounds. In butter, the protein, carbohydrate, and mineral salts are in the buttermilk, which is finely dispersed throughout the mass of butterfat. As pointed out by Rahn and Boysen (100) these particles may be extremely small and so numerous that the majority of the droplets of buttermilk are sterile. Further, some of the droplets may be largely water with the slightest traces of foodstuffs, if any, unless the spores of the molds have germinated and produced sufficient mycelium and enzymes to attack the abundant supply of adjacent fat.

Moisture

It is generally recognized that moisture is necessary for the germination of the spores of molds and that the development of hyphae is accelerated when sufficient moisture is available. In order to utilize any foodstuff, water in sufficient quantities must be present. This has been indicated in connection with the availability of fat as a nutrient for fungi.

Moisture in substrate.—Batten and Bywaters (9) prepared a series of blocks of cacao butter containing from 0 to 20 per cent of water in an emulsified state and inoculated mold cultures into the center of the blocks. Under these conditions, the growth of the mold was slow, no matter how high the percentage of water. This may have been explained by other factors, such as a lack of suitable food or oxygen. Mold did develop on solidified emulsions of cacao butter and water (about 30 per cent) when spores were inoculated on the surface. Burr and Wolff (19) found that when butter contained water in large droplets instead of being in the normal, finely divided state described by Boysen (15) and Rahn and Boysen (100), mold development was favored. They pointed out that nutrients were not available unless sufficient moisture was present. Combs and Eckles (23) made the statement that moisture content is a factor governing the development of molds in butter. As pointed out elsewhere, Duclaux (36) found that water was required for the germination of mold spores. According to Gripenberg (53), wood and paper used in butter packages sustained the growth of molds when sufficient amounts of moisture were present. Hood and White (60) were of the opinion that normal butter contained sufficient moisture for mold development. This seems to be certain, as the moisture in butter is present largely in connection with the principal food consituents such as proteins, carbohydrates, and mineral matter. In his investigations on the causes of rancidity of vegetable margarine, Jacobson (62) found that oils become rancid through mold action when small quantities of water (0.2 to 0.5 per cent) were present. König, Spieckermann, and Bremer (68) reported that a multiplication of molds occurred in three sorts of cottonseed meal only when the water content was higher than 14 per cent. McWeeney (80) warned against superfluous moisture in butter if molding were to be prevented. As pointed out elsewhere, Patil and Hammer (92) observed the development of microörganisms in butterfat and ghee only when water was present with these substances. Thom and Shaw (140) reported mold in butter with a water content ranging from 7.38 to 18 per cent. According to Welte (145), *Penicillium glaucum* made good growth after 4 days on bread containing 33 per cent of water, but less satisfactory development in 6 days when the water content was 20 to 25 per cent. With *Aspergillus nidulans*, no growth was obtained, even after 6 days, when 25 per cent or less of moisture was present. He quoted Flügge as authority for the statement that mold growth was completely hindered when the water content was as low as 10 to 12 per cent.

It is evident that water in the substrate is essential for the development of molds. Just what the minimum moisture requirement may be under different conditions is not so clear. The fact remains, however, that normal butter contains a high percentage of moisture in proportion to the most easily utilized food constituents and should provide a satisfactory substrate for mold growth from the standpoint of moisture.

Moisture in atmosphere.—The matter of humidity is another consideration of some importance. Combs and Eckles (23) held that the moisture content of the atmosphere in which butter was stored had a considerable influence upon the development of molds. This is in agreement with the observations of Orla-Jensen (63) that *Cladosporium butyri, Oidium lactis,* and *Penicillium glaucum* grew best when butter was kept in a moist room. According to König, Spieckermann, and Bremer (68), molding was increasingly abundant with an increase in humidity. Macy and Pulkrabek (81) stored samples of unsalted butter wrapped in mold-contaminated parchment under conditions of varying humidity. Nineteen samples kept at 1° C. for 50 to 60 days at approximately 70 per cent relative humidity showed no mold. The same was found true of ten samples stored at 12° C. for 30 days at about this humidity; two other samples at the same temperature and humidity after 50 to 80 days were moldy. A high relative humidity (90 to 100 per cent) favored the growth of molds upon comparable samples kept at the same temperatures. Thom and Shaw (140) found that samples of butter inoculated with various molds and kept at room temperature for several days showed no growth of mold at ordinary humidities, but when the samples were placed in a moist chamber the growth was active. At the low humidities none of the cultures appeared to develop, regardless of the moisture content of the butter. The failure of mold to grow on butters with high protein content when kept at low humidities indicated that the moisture in the atmosphere was the essential factor, as the cultures developed in the moist chamber in butters with a low protein content. Studies were also reported in which definite humidities, namely, 100, 90, 79.6, and 69.6 per cent were employed. The growth of molds was found to be greatest at 100 per cent, good at 90 per cent, considerable at 79.6 per cent, and little or none at 69.6 per cent relative humidity. Unquestionably, humidity is a very important factor in the growth of molds in butter.

Atmosphere

The importance of a sufficient supply of oxygen for the development of molds in butter has been suggested by a number of investigators, among whom are, Boekhout and de Vries (12), Burr (18), Burr and Wolff (19), Duclaux (36), Gripenberg (53), Hood and White (60) and Rogers (108).

Lopriore (78) observed that the germination of spores of *Mucor mucedo* was slowed by the presence of 10 per cent carbon dioxide in the atmosphere. Undiluted CO_2, altho producing total inhibition, did not kill the spores even after an exposure of three months. The formation of sporangia was more readily suppressed than spore germination. Brown (17) reported that within quite wide limits, the oxygen pressure had very little effect upon the germination and growth of certain molds, such as Botrytis, Fusarium, and Alternaria. The germination and growth of these organisms was retarded by CO_2, especially at lower temperatures with a scanty food supply.

According to Porodko (95), it did not appear that aerobic organisms such as *A. niger*, *P. glaucum*, and *M. stolonifer* were particularly sensitive to changes in oxygen pressure. Sevenster (120) (121) (122) stated that butter stored under vacuum was not in a favorable environment for the growth of molds.

Karsner and Saphir (65) studied the effect of high partial pressures of oxygen upon several species of molds grown on Sabouraud's agar in petri dishes kept in glass jars. They found that concentrations of oxygen of 76 per cent or more exercised a definite inhibitory effect upon some molds.

Rippel and Bortels (106) observed that the development of *Aspergillus niger* from spores was hampered by removing the CO_2 from the atmosphere. They held that CO_2 was necessary for the functioning of plant cells.

According to Rockwell and Highberger (107) a species of Mucor was found to be inhibited in growth when incubated at 37° C. in a jar containing 4 per cent NaOH to remove some of the CO_2 from the atmosphere.

The notion that molds are strict aerobes seems to be faulty, but it is evident that they do require some oxygen for their normal development, altho excessive quantities are inhibitory. How important these facts may be in connection with the molding of butter is not fully explained. One must bear in mind that a certain amount of air is entrapped in ordinary butter, the amount and distribution varying at different times as shown by Rahn and Mohr (102). The extent of the surface of butter exposed to the air also may be a factor. Reisz (104) has shown that a cylinder (r^2 h) of butter exposes 14.5

per cent and a cube (r^3) 24.1 per cent more surface than a sphere ($4/3\ r^3$). If air is essential for the development of mold in butter, the shape of the package may be worthy of consideration.

Temperature

Temperature profoundly influences the growth of microörganisms. Molds are no exception to this.

Welte (145) reported that *Penicillium glaucum* and *Mucor stolonifer* showed the best growth at room temperature; *Aspergillus nidulans* grew well at 36° to 37° C. In his studies on *Aspergillus niger* and *Penicillium glaucum*, Thiele (135) observed that the maximum temperature for growth was not constant and depended upon the medium. The minimum for *P. glaucum* was 1.5° to 2.0° C. and for *A. niger*, 6° to 8° C. Later, he reported (136) that *P. glaucum* made only scanty growth at 30° to 40° C. Thom (137) found that few Penicillium species grew normally at 37° C. but nearly all showed rapid growth at 12° to 30° C. The development was progressively reduced by lower temperatures. At 10° to 20° C. it was slow but good, while at temperatures approaching 0° C. the growth was very much slower. Ames (3), in studying the minimum temperature for germination of spores of *Monilia fructigena*, *Penicillium digitatum*, *Rhizopus nigricans*, and other storage-rot fungi, found that the spores of these species had a minimum germination point at 1° C., 1° C., and 3° C. while their optimum temperatures for growth were 25° C., 25° C., and 35° C., respectively. He pointed out that the minimum temperature for fructification in all cases was several degrees higher than that for growth. Brooks and Cooley (16) determined that the spores of *Alternaria sp.*, *Botrytis cinerea*, and *Penicillium expansum* germinated slowly at 0° C. on cornmeal agar. *Aspergillus niger* failed to germinate at 10° C. Meyer (84) advanced the opinion that it was not permissible to speak of an optimum temperature for the growth of fungi except in the sense that it was the temperature which permitted the greatest rate of growth under strictly specified conditions other than temperature.

These reports are representative of many that indicate that each species shows different responses to different temperatures for germination, growth, or fructification.

In respect to the growth of molds in butter at different temperatures, the reports are largely in generalities, altho Boekhout and de Vries (12) reported that moldiness had appeared in samples of butter stored at —3° to —6° C. for 4 weeks to 4½ months. A report from the United States Department of Agriculture (6) recommended that butter be stored below 2° F. (—16.67° C.) to prevent mold development. Hood and White (60) pointed out that molds grew in butter over a wide range of temperatures but were checked at temperatures approaching the freezing point of water. This was in agreement with the views of Rogers (108) expressed several years before. Macy and Pulkrabek (81) observed that temperature was a factor which influenced the development of mold on experimental butters. Stokoe (129) remarked that temperature entered into the factors favoring the production of rancidity of oleomargarine by molds, on the basis that this defect was more prevalent in the summer months.

In a general way it appears evident that low temperatures impede the development of molds in butter but experimental evidence for different species and specific temperatures is lacking. Butter has been found to be moldy even at relatively low temperatures when stored for sufficient periods of time.

Miscellaneous Chemical and Physical Environment

Many factors may be considered under this category, but only a few will be discussed.

Salt.—Investigations have been undertaken regarding the effect of salt (sodium chloride) upon the growth of molds. Eschenhagen (43) reported that *Aspergillus niger* would grow in a 17 per cent solution of sodium chloride in an inorganic medium, Penicillium at 18 per cent, and *Botrytis cinerea* at 12 per cent. Kosinski (69) was of the opinion that a 0.26 molar solution (1.523 per cent) of sodium chloride did not affect the respiration of *Aspergillus niger*. According to Gustafson (54), spores of *Aspergillus niger* failed to germinate in 0.5 molar solution of sodium chloride (about 3 per cent). Lindet (76) explained the antiseptic action of salt upon the basis of its depriving microörganisms of a portion of their elementary structure through plasmolysis. Wöltje (146) studied the effect of various concentrations of sodium chloride in different media upon the growth of eighteen species of Penicillium. The killing concentration of salt at 15° to 17° C. for conidia was found to be from 6 to 26 per cent and for mycelium from 8 to 27 per cent, depending upon the species. Extensive microscopic studies of the effect of salt upon the growth of *Penicillium expansum, Alternaria solani,* and *Oidium lactis* were reported by Bitting (11). She found that salt retarded growth and stunted development. It took longer for the conidia to germinate in higher salt concentrations. *Oidium lactis* was most susceptible and did not grow in 15 per cent salt. Molliard (85) found that sodium chloride at concentrations up to 10 per cent lowered the activity of *Sterigmatocytis nigra*. Golding (51) studied four species of Penicillium isolated from blue-veined cheese and inoculated into sweet skimmilk and Czapek's medium containing 4, 8, 12, and 16 per cent of salt. The salt decreased the power to digest casein as well as the growth of these organisms.

Observations have been made in a general way upon the effect of salt on the appearance of mold in butter. Alvord (2) reported that unsalted butter exported to England from the United States became moldy. Dean and Harcourt (29) found that salt was more effective in preventing mold than other preservatives. Burr and Wolff (19) (20) reported that salted butter with a normal curd content was not an exceptionally good substrate for molds and that mold spores could not germinate well when 2 per cent salt was present in the butter. Species of Mucor did not develop in salted butter and the growth of Penicillium was retarded. Rahn, Brown, and Smith (101) found that *Oidium lactis* increased in unsalted but not in salted butter. The keeping quality of butter and margarine was improved when they contained about 3 per cent of salt according to Fischer and Gruenert (48). Hastings (59) held the opinion that mold spores could not germinate in salted butter. Combs and Eckles (23) also concluded that the salt content of butter had a considerable influence upon the development of mold. Jacobson (62) reported that vegetable margarine was well preserved only when salt or other preservative was dissolved in the water droplets so that the molds were restrained. Abbott and Ashenfelter (1) made the observation that mold counts increased more rapidly in unsalted than in salted butter. The idea that heavy salting of liners, wrappers, tubs, etc., as well as the soaking of parchment paper in brine decreased the possibilities of the development of mold upon the surface of butter or package has been upheld by anonymous writers (4), (6), (7) and by Böggild (13), Burr (18), Davis (27), Dean (28), Ibsen (61), Rogers (108), and Zoffman (148).

More detailed studies of salt effects, with special reference to the butter industry, have been undertaken. As reported elsewhere, Siedel (124) attributed to the action of molds, the roquefort, turnipy, or beet flavor that developed in granular butter immersed in 10 per cent and saturated brine. While he did not record actual visible growth, he implied that some development had occurred. Gripenberg (53) made use of a butter "serum," which consisted of the portion of butter removable after butter was melted and most of the fat decanted. When this serum contained 18 and 20 per cent of salt, molds (*Penicillium sp.* and *Trichosporium sp.*) were found growing in it after 5 to 6 months. When this material was diluted, the fungi grew much better. Hanging drops of butter serum containing 0, 10, and 25 per cent of salt were inoculated with *Penicillium crustaceum* and *Trichosporium collae*. In the unsalted serum, growth was active after 9 days for both types; with 10 per cent salt the growth was slight; with 25 per cent no signs of growth were evident. Parchment paper dipped in salted butter serum showed no molding in the 24 per cent serum but increasingly heavy growth with decreasing amounts of salt. McKay and Larsen (79) studied the growth of *Penicillium glaucum* in media containing various quantities of salt. The growth after 2 days was luxuriant with less than 9 per cent salt present, noticeable with 9 per cent, but only a trace with 10 per cent salt. Fettick (45) followed the development of *Oidium lactis* and *Penicillium glaucum* in unsalted butter and in butter containing 3 per cent salt by plating samples at the beginning of the storage period and after 7 weeks, 2 months, and 4 months. In the salted butter the molds decreased immediately and disappeared within the 2 months; in the unsalted sample, they increased steadily. He also prepared sterile butter containing 0, 0.5, 1, 2, 3, 4, 5, and 6 per cent of salt. These samples were inoculated with *Oidium lactis, Mucor mucedo,* and *Penicillium glaucum* and stored for one week in a dark place at 17° C. Platings were made at the end of this period. All three species decreased in proportion to the increased percentage of salt. No growth appeared in samples containing 4 per cent or more of salt. The effect of various percentages of salt in Czapek's medium was studied by Thom (138). Petri plate cultures were prepared of twenty-one species of Penicillium and ten of Aspergillus, using Czapek's solution with and without agar, and containing 10 per cent of sodium chloride. After 19 days all the Penicillium and Aspergillus cultures had grown on the solid medium, but only sixteen of the Penicillium and nine of the Aspergillus cultures in the liquid. The extent of growth varied with the different species. Growth of *P. pinophilum, P. lilacinum, P. luteum, P. digitatum, P. purpurogenum, P. roseum, P. duclauxii, A. nidulans, A. fumigatus,* and a check culture of *O. lactis* was stopped or reduced to a negligible amount in the liquid medium. Further, twelve species of Penicillium were inoculated on Czapek's medium containing 0, 5, 10, and 15 per cent of sodium chloride. After 34 days, growth had occurred in all samples reported. There was relatively less development, however, with increasing percentages of salt. It was determined that *Oidium lactis* was reduced to negligible growth when the amount of salt exceeded 6 per cent.

Thom and Shaw (140) investigated the growth of three cultures of Alternaria, four of Mucor, two of *P. roqueforti,* and individual cultures of the following, *Cunninghamiella sp., Fusarium sp., O. lactis, Penicillium sp., P. expansum, P. stoloniferum, P. chrysogenum, P. purpurogenum, Rhizopus nigricans, Trichoderma sp.,* and a red mold on Czapek's agar containing 6.5 per cent and 14.4 per cent of salt. The plates were kept in a moist chamber. All grew in 6.5 per cent of salt, Oidium least and Penicillium most. In 14.4 per cent of salt, Alternaria and Penicillium alone developed, the latter showing the better growth. In an 18 per cent salt Czapek's agar, three species of Penicillium and *Aspergillus repens* grew; in 21 per cent the spores of *P.*

chrysogenum were the only ones to germinate. Thom and Shaw noted that the growth was better on salted agar than on salted butter of the same percentage of salt. Denning (30) found butter in good condition after 8 months' storage at 50° F. in a 20 per cent solution of sodium chloride. Later experiments (31) indicated that butter kept in 30 per cent of salt had been preserved in good condition. *Hormodendrum cladosporioides* cultures were seeded by Boekhout and de Vries (12) into a medium containing peptone, levulose, and nutrient salts and varying quantities of sodium chloride. Five cultures grew in the medium containing 13.4 per cent salt, four in 14.3 per cent, two in 16 per cent, two in 17 per cent, and none in 18, 19, or 20 per cent. Samples of butter containing 0, 2, 2.5 and 3 per cent of salt were placed in Erlenmeyer flasks at 21° C. and held for one month after being inoculated with two Hormodendrum cultures. Growth occurred only on the unsalted butter. It is evident that Boekhout and de Vries obtained better growth on the salted, synthetic medium.

Paraschtschuk (90) (91) studied the growth of several species of mold on malt agar containing varying percentages of salt and found that *Penicillium glaucum* and *Cladosporium herbarum nigr.* were able to develop when the salt concentration was as high as 18 per cent.

According to the foregoing evidence, the influence of salt varies, however, depending upon the species and the substrate. Altho unsalted butter is most commonly affected, mold often appears on salted butter. This occurrence demands explanation.

Degree of acidity.—Schaffer (115) stated that the growth of molds was rather favored by the low acidity of butter made from pasteurized cream. According to Laxa (73) the presence of lactic acid did not hinder markedly the peptonization of casein by molds. In studies carried on by Boekhout and de Vries (12) two cultures of *Hormodendrum cladosporioides* were grown on a base medium containing lactic acid. One culture was checked by 0.75 per cent lactic acid; the other not until the percentage of acid reached 1.0 per cent.

None of these investigations were based upon carefully controlled conditions in butter, so give no satisfactory idea of the effect of acidity in butter upon the growth of molds.

Many papers dealing with the effect of hydrogen-ion concentration upon the development of molds have been presented in recent years. Only two are mentioned here. Gustafson (55) studied the effect of various hydrogen-ion concentrations upon the respiration of *Penicillium chrysogenum*. He found that the rate of respiration was not affected within the range of pH 4.0 and pH 8.0. Johnson (64) at the Iowa station, reviewed previous investigations and reported that the acid and alkaline reactions inhibiting the growth of seven molds ranged from pH 1.6 to pH 11.2 depending upon the species.

These investigations indicate that most molds grow over a wide range of hydrogen-ion concentrations. Most species are favored by an acid medium, and the limits of acidity reached in ordinary butter are such that the hydrogen-ion concentration, as such, should not have much influence on mold development. The nature of the substances bringing about the changes in pH appears to be of much greater significance.

Light.—Altho the general opinion, expressed by Rogers (108), that molds developed much better in the dark than in the light, has been held by most investigators, Kolkwitz (67) and Maxinow (82) suggested that at times light accelerated the metabolism of fungi. In practice, however, butter is kept in packages and in storage rooms where light does not gain direct access to it. Consequently, light would not be expected to influence the growth of molds on butter.

Vitamins.—There have been some investigations into the effect of growth-stimulating substances, such as vitamins, upon the development of molds. Linossier (77) pointed out that *Oidium lactis*, *Aspergillus niger*, and *Penicillium glaucum* were able to grow in pure culture in media lacking vitamins but containing necessary nutrients. When the nutrients were greatly reduced, the addition of vitamin-containing substances, such as orange juice, sometimes stimulated growth. Lepeschkin (75) reviewed the literature on the subject and concluded that vitamins were not of great importance in the nutrition of molds.

At any rate, butter ordinarily contains vitamins and in sufficient quantities and variety to satisfy the slight demands of the fungi.

Species of Molds Isolated from Butter

Many species of molds have been isolated from butter but they have not always been shown to be the specific causes of defects in appearance, flavor, or aroma. The species of molds are important, as one must determine what types actually grow in butter even under the most favorable conditions. Many forms encountered when butter is plated may exist in butter only in the form of spores, which do not germinate under the conditions existing in the product. Every species should be studied to determine whether or not it can develop in ordinary butter.

It is not necessary to present anything more than a catalog of some of the species that have been isolated from butter, giving the species name applied by the investigator who reported it and the key number to locate the authority in the bibliography. In addition, attention may be called to the fact that See (119) described several species isolated from paper. It is possible that some of these might be found on parchment paper used for wrapping butter.

Alternaria sp. (22) (140); *Aspergillus sp.* (18) (26) (90) (91) (128) (129); *Aspergillus flavus* (9); *Aspergillus glaucus* (113) (129); *Aspergillus niger* (19) (62); *Aspergillus oryzae* (9); *Botricanus scostan* (90) (91); *Botrytis sp.* (58); *Chaetomium sp.* (36); *Cladosporium sp.* (90) (91) (129) (140); *Cladosporium butyri* (62) (63); *Cladosporium herbarum* (80) (90) (91); *Coniosporium sp.* (26); *Coniothecium sp.* (26); *Dematium sp.* (70); *Dematium pullulans* (80); *Epicoccum sp.* (22); *Eurotium repens* (68); *Eurotium rubrum* (68; *Hormodendrum cladosporioides* (12); *Monilia sp.* (83) (90) (91) (96); *Monilia alba* (90) (91); *Monilia candida* (90) (91); *Monilia roseum* (90) (91); *Mucor sp.* (18) (22) (53) (56) (58) (90) (91) (105) (140); *Mucor hiemalis* (90) (91); *Mucor mucedo* (5) (19) (46) (57) (133); *Mucor petrinsularis* (36); *Mucor racemosus* (90) (91); *Mucor spinosus* (36); *Mucor sylvaticus* (90) (91); *Oidium lactis* (5) (8) (22) (39) (45) (58) (63) (83) (86) (87) (88) (89) (90) (91) (96) (101) (105) (113) (133) (140); *Oidium variicolor* (97); *Oospora ruberrima* (111); *Penicillium sp.* (18) (19) (26) (35) (53) (58) (90) (91) (105) (128) (131); *Penicillium brevicaule* (142) (144); *Penicillium chrysogenum* (139); *Penicillium crustaceum* (53) *Penicillium expansum* (140); *Penicillium glaucum* (5) (9) (19) (36) (39) (40) (45) (46) (62) (63) (70) (90) (91) (113) (129) (130) (133); *Penicillium olivaceum* (?) (80); *Penicillium roqueforti* (22) (70) (140); *Rhizopus arirus* (90) (91); *Stemphylium butyri* (93) (123) (140); *Sterigmatocystis sp.* (36); *Stilbaciae graphium* (90) (91); *Trichosporium collae* (53); *Verticillium sp.* (36).

EXPERIMENTAL

Purpose of Study

The purpose of the studies reported on subsequent pages was to determine the influence of certain factors upon the growth of molds with special reference to their development in butter; and to investigate some of the basic considerations with a hope that the results might offer opportunities for their interpretation in terms of the complex inter-relationships of the various factors that appear to be operating in such a valuable and concentrated food as butter. It was anticipated that many phenomena would appear to throw light on some of the perplexing problems at present recognized and to serve as bases upon which further studies might rest.

Method of Procedure

In the beginning, it was necessary to decide what factors appeared to be most important in their influence upon the growth of molds, particularly in butter. These were as follows: (1) Food supply, (2) moisture, (3) temperature, (4) atmosphere, and (5) miscellaneous chemical and physical factors, especially the effect of various concentrations of sodium chloride.

Species of Molds Used in Experiments

In order to have one fixed condition throughout the experiments, ten species of molds were selected to be used in the studies. These cultures were representative of types of molds found commonly in butter. As a convenience in the presentation of the experimental data, reference will be made to them by number. These cultures and their corresponding key numbers are as follows:

1. *Alternaria humicola* Oudemans
2. *Aspergillus flavus* Link
3. *Aspergillus niger* Van Tieghem
4. *Hormodendrum cladosporioides* (Fresenius) Saccardo
5. *Mucor sylvaticus* Hagem
6. *Oospora lactis var. A.* (Fresenius) Lindau
7. *Oospora lactis var. B.* (Fresenius) Lindau
8. *Penicillium biforme* Thom
9. *Penicillium expansum* Link
10. *Rhizopus nigricans* Ehrenberg

The Mucor and Rhizopus stock cultures were carried on potato-dextrose agar, the Oospora cultures on whey agar, and the rest on Czapek's agar. These media gave the most luxuriant growth for the particular species. Inoculations in the various experiments were made directly from cultures 10 days to 2 weeks in age, particular care being taken to transfer none of the culture medium.

Methods Employed in Experiments

The methods employed for preparing the different substrata, for maintaining the desired temperature, humidity, etc., will be discussed under the respective subdivisions of the material presented.

Manner of Recording Results

The extent of growth made by the ten species on different substrata and under other varying conditions will be recorded uniformly by the following symbols:

−	No visible growth
±	Questionable growth
+	Slight, visible growth
++	Moderate growth
+++	Abundant growth
++++	Normal growth

Note: Wherever these symbols are in parentheses, they indicate subsurface growth.

In a similar manner, the color produced by the cultures under the various conditions will be registered according to the following symbols:

W —White
Y —Yellow
G —Green
B —Black
Br—Brown
C —Cream

EXPERIMENTAL RESULTS

The experimental data will be presented under the following subdivisions:

A. Food supply
    1. Fats and related substances
    2. Proteins and related substances
    3. Carbohydrates and related substances
    4. Mineral constituents
    5. Combinations of 1, 2, 3, and 4
B. Moisture
    1. Moisture in substrate
    2. Moisture in atmosphere
C. Temperature
D. Atmosphere
    1. Ordinary air supply
    2. Reduced air supply—partial vacuum
    3. Partial removal of carbon dioxide
    4. Removal of oxygen
E. Miscellaneous chemical and physical factors
    1. Salt content

A. Food Supply

The primary requirement for the growth of microörganisms is a satisfactory food supply. Butter furnishes a variety of foodstuffs, principally fat, but also proteins, carbohydrates, and mineral salts in varying amounts. Each of these constituents has been studied as a source of food for the ten species of molds previously selected.

1. Fats and Related Substances

a. Fresh Butterfat

Methods. Fresh unsalted butter was melted at a temperature of 50° to 55° C. and placed in a warm, separatory funnel. The curd and water that settled out were drawn off. The fat was washed five times in the funnel by shaking with it equal quantities of water at 60° to 65° C. After each washing, the mixture was allowed to stand until the layers of fat and water were distinct, whereupon the water was drawn from the funnel. The washed fat was tempered to 55° C. and left at this temperature for 24 hours, during which time it was filtered through filter paper to remove traces of water. The filtered fat was tubed in 10-cc. amounts and autoclaved. When ready to use, the fat was melted and poured into sterile petri plates and solidified quickly. Analyses of the autoclaved fat showed it to be water-free. The cultures were streaked across the surface of the fat as uniformly as possible. The plates were placed in piles on a rack in a humidor consisting of a 10-gallon, covered earthenware crock in the bottom of which was a one-inch layer of water containing sufficient bichloride of mercury to maintain it as a sterile fluid. The relative humidity, determined by a wet-dry bulb hydrometer, was maintained at 100 per cent. The temperature of incubation ranged from 20° to 25° C.

TABLE I

Growth of Mold Cultures on Fresh Butterfat

Culture	Extent of growth at 20–25° C., high humidity, after						
	4 days	1 week	2 weeks	3 weeks	4 weeks	6 weeks	6 weeks
	Visible						Microscopic
1. *Alternaria humicola*	—	—	—	—	—	—	—
2. *Aspergillus flavus*	—	—		—	—	—	—
3. *Aspergillus niger*	—	—	—	—	—	+B	+
4. *Hormodendrum cladosporioides*	—	—	—	—	—	—	+
5. *Mucor sylvaticus*	—	+	+	+	+	+	+
6. *Oospora lactis var. A.*	—	—	—	—	—	—	—
7. *Oospora lactis var. B.*	—	—	—	—	—	—	+
8. *Penicillium biforme*	—	—	—	—	—	—	+
9. *Penicillium expansum*	—	—	—	—	—	—	+
10. *Rhizopus nigricans*	—	—	—	—	—	—	—
Check	—	—	—	—	—	—	—

Results. The extent of growth in the fresh butterfat is indicated in Table I. After one week the only visible growth was noted with Culture 5 and it was evident that development was restricted to the point of inoculation, where sufficient residual nutriment may have been present in the mycelium inoculated. At the end of 6 weeks, Culture 3 had produced a few black sporangia; Culture 5 had shown no further increase, rather a slight diminution in the mass of growth. A microscopic examination of the plates after 6 weeks incubation revealed signs of germination of the conidia in Cultures 3, 4, 5, 7, 8, and 9, but very little hyphal development except in Culture 5, where the mycelium had developed extensively.

b. Old Butterfat

Methods. The method for preparing the old butterfat was the same as that described for fresh butterfat. The butter used was unsalted, one month old, and decidedly cheesy in flavor. The surface was discolored with spots of mold. The conditions for inoculation and incubation were the same as those for the fresh butterfat.

Results. As shown in Table II, growth was evident after 4 days in Cultures 3 and 8, but again this development was at the point of inoculation. Culture 3 produced a few black sporangia; Culture 8 formed a light green spot. At the end of one week, Culture 10 showed slight aerial mycelium, which disappeared within the following week. Culture 1 began to produce a green spot after 3 weeks. This became deeper in color during the subsequent period. Culture 9 developed a small green spot after the third week. A dark green streak appeared along the line of inoculation in Culture 4 at the expiration of the 6 weeks. The microscopic examination indicated that Cultures 1, 2, 3, 4, 8, and 9 had made slight growth during the trial. In general, the growth on this type of butterfat was somewhat better than that on the fresh butterfat.

TABLE II

Growth of Mold Cultures on Old Butterfat

Culture*	Extent of growth at 20–25° C., high humidity, after						
	4 days	1 week	2 weeks	3 weeks	4 weeks	6 weeks	6 weeks
	Visible						Microscopic
1. *Alt. humicola*	—	—	—	+G	+	+	+
2. *A. flavus*	—	—	—	—	—	—	+
3. *A. niger*	+B	+	+	+	+	+	+
4. *H. cladosporioides*	—	—	—	—	—	+G	+
5. *M. sylvaticus*	—	—	—	—	—	—	—
6. *O. lactis var. A.*	—	—	—	—	—	—	—
7. *O. lactis var. B.*	—	—	—	—	—	—	—
8. *P. biforme*	+G	+	+	+	+	+	+
9. *P. expansum*	—	—	—	—	+G	+	+
10. *R. nigricans*	—	+W	—	—	—	—	—
Check	—	—	—	—	—	—	—

* Abbreviations used in this and subsequent tables are as follows: Alt.=Alternaria, A.=Aspergillus, H.=Hormodendrum, M.=Mucor, O.=Oospora, P.=Penicillium, R.=Rhizopus.

c. Butterfat from Washed Cream

Methods. Four pounds of 30 per cent sweet cream were diluted to 3 gallons with ordinary tap water and heated to 35° C. The diluted cream was then separated in a centrifugal separator. The resultant cream was again diluted in the same way, heated, and separated. The process was repeated until the cream had been diluted and separated ten times. The cream that was finally obtained was placed at 12° C. and allowed to stand over night. During this period the fat had formed a solid mass, floating above a slightly cloudy serum. The mixture was heated to 50° C. and placed in a warm separatory funnel. In this way it was possible to remove the serum. The fat was washed five times with water at 60° to 65° C. Thereafter, it was placed at 55° C. for 24 hours, during which time it was allowed to filter through ordinary filter paper. An analysis showed that all water had been removed. The fat was placed in test tubes and autoclaved. When desired for use the fat was melted, poured into petri plates, and solidified promptly. Conditions of inoculation and incubation were the same as those described in the preceding experiments.

Results. As in the previous experiment, Cultures 3 and 8 gave evidence of growth after 4 days, according to the data presented in Table III. Culture 10 had developed a noticeable aerial mycelium during this period but, as happened before, this mycelium gradually disappeared. A scanty aerial mycelium was sent up by Culture 5 after one week, but this likewise disappeared after 4 weeks. A green streak following the line of inoculation of Culture 4 appeared at the end of 4 weeks, while Culture 9 had produced a slight green spot during the same period. The microscopic examination made after 6 weeks showed that Cultures 2, 3, 4, 5, 8, 9, and 10 had been able to develop slightly near the point of inoculation.

TABLE III

Growth of Mold Cultures on Butterfat from Washed Cream

Culture	Extent of growth at 20–25° C., high humidity, after						
	4 days	1 week	2 weeks	3 weeks	4 weeks	6 weeks	6 weeks
	Visible						Microscopic
1. *Alt. humicola*	—	—	—	—	—	—	—
2. *A. flavus*	—	—	—	—	—	—	+
3. *A. niger*	+B	+	+	+	+	+	+
4. *H. cladosporioides*	—	—	±	±	+G	+	+
5. *M. sylvaticus*	—	+W	+	+	+	—	+
6. *O. lactis var. A.*	—	—	—	—	—	—	—
7. *O. lactis var. B.*	—	—	—	—	—	—	—
8. *P. biforme*	+G	+	+	+	+	+	+
9. *P. expansum*	—	—	—	±	+G	+	+
10. *R. nigricans*	+W	+	—	—	—	—	+
Check	—	—	—	—	—	—	—

d. Butterfat Washed with Alcohol

Methods. A portion of the fresh butterfat used in the experiment reported in Table I was mixed with equal parts of 95 per cent ethyl alcohol and shaken thoroly. The fat was drawn off by means of a separatory funnel, placed at 55° C. and filtered through paper, after which it was placed on a water bath to drive off any remaining alcohol. The final analysis showed no traces of water in the fat. The fat was tubed and autoclaved. When desired, it was melted and poured into petri dishes, where it solidified. The fat was inoculated as described in preceding experiments.

Results. Table IV gives the results of the experiment. Culture 3, as before, produced a few black sporangia after 4 days. At the end of one week, Culture 5 had sent forth scanty aerial mycelium but, as had happened in the previous experiments, this disappeared after 4 weeks. Culture 2 appeared to grow on this preparation of butterfat and after one week a few yellowish-green sporangia were visible. After 3 weeks, Culture 4 developed to such an extent that green streaks were evident, and Cultures 8 and 9 produced green spots. Finally, at the end of 6 weeks, Culture 1 produced a small green spot. The microscope revealed extensive development of Culture 4 and slight mycelial growth of Cultures 1, 2, 3, 8, and 9. In general, the growth was slightly better in the fat washed with alcohol than on the other preparations.

TABLE IV

GROWTH OF MOLD CULTURES ON BUTTERFAT THAT HAD BEEN WASHED WITH ALCOHOL

Culture	Extent of growth at 20–25° C., high humidity, after						
	4 days	1 week	2 weeks	3 weeks	4 weeks	6 weeks	6 weeks
	Visible						Microscopic
1. *Alt. humicola*	—	—	—	—	—	+G	+
2. *A. flavus*	—	+G	+	+	+	+	+
3. *A. niger*	+B	+	+	+	+	+	+
4. *H. cladosporioides*	—	—	—	+G	+	+	++
5. *M. sylvaticus*	—	+W	+	+	+	—	±
6. *O. lactis var. A.*	—	—	—	—	—	—	—
7. *O. lactis var. B.*	—	—	—	—	—	—	—
8. *P. biforme*	—	—	—	—	+G	+	+
9. *P. expansum*	—	—	—	—	+G	+	+
10. *R. nigricans*	—	—	—	—	—	—	—
Check	—	—	—	—	—	—	—

e. Fresh Butterfat Plus Water

Methods. The fresh butterfat, as prepared in experiment "a" described previously, was used in the trial. In order to provide a substrate in which the fat and water might be more intimately associated and in a more finely divided state, a medium containing 1.5 per cent of washed agar was prepared. Fifteen grams of Bacto agar were placed in a cloth bag and suspended in running water over night in order to remove some of the soluble and finely divided impurities. After the washed agar had been dried at 55° C. it was weighed and sufficient distilled water added to make a 1.5 per cent concentration of agar. This became a substrate, which supplied sufficient water but little nutriment. Similar batches of the same medium were prepared at various times, some containing 1.0 per cent and some 1.5 per cent of agar, depending upon circumstances. This medium was placed in test tubes in measured amounts and autoclaved. When ready for use in combination with the fat, the agar and fat were melted and the butterfat was added to the agar in the proportions of four parts of agar to one part of fat. The mixture was shaken thoroly until the fat was in a finely divided state, then poured into petri dishes and cooled on cold surface as quickly as possible. The droplets of fat were evenly dispersed throughout the solidified agar. The fat-agar mixtures were inoculated by streaking the cultures across the surface. The plates were stored at room temperature (20° to 25° C.) for 4 weeks at a relative humidity varying from 60 to 65 per cent.

Results. The fact that molds made very meager growth on the washed agar substrate is indicated in Table V. The results reported are representative of other lots of the same medium used in later experiments. Very slight growth was obtained at any time, and in most cases it was barely visible, especially on the surface, altho a slight penetration of the mycelium below the surface was noted in some instances. As shown in Table VI, the presence of water led to much more extensive growth of all the cultures except 6 and 7. Cultures 1, 3, and 4 grew especially well. It is significant that Cultures 8 and 9 were able to produce a more or less typical odor of Roquefort cheese before any growth was visible.

TABLE V

GROWTH OF MOLD CULTURES ON 1.5 PER CENT WASHED AGAR SUBSTRATE

Culture	Extent of growth at 20–25° C., ordinary humidity, after					
	4 days	1 week	2 weeks	3 weeks	4 weeks	4 weeks
	Visible					Microscopic
1. *Alt. humicola*	+W	+	+	+	+	+
2. *A. flavus*	+	+	+	+	+	+
3. *A. niger*	+	+	+	+	+	+
4. *H. cladosporioides* ..	+	+	+	+	+	+
5. *M. sylvaticus*	+W	+	+	+	+	+
6. *O. lactis var. A.* ...	—	—	—	—	—	—
7. *O. lactis var. B.* ...	—	—	—	—	—	—
8. *P. biforme*	±	+	+	+	+	+
9. *P. expansum*	±	±	±	±	±	+
10. *R. nigricans*	+W	+	+	+	+	+
Check	—	—	—	—	—	—

TABLE VI

GROWTH OF MOLD CULTURES ON A MIXTURE OF 1.5 PER CENT WASHED AGAR AND FRESH BUTTERFAT

(4 parts of agar medium: 1 part of butterfat)

Culture	Extent of growth at 20–25° C., ordinary humidity, after					
	4 days	1 week	2 weeks	3 weeks	4 weeks	4 weeks
	Visible					Microscopic
1. *Alt. humicola*	+W	+	++G	++	++	+
2. *A. flavus*	—	+Y	+YG	+	+	+
3. *A. niger*	+B	++	++	++	++	+
4. *H. cladosporioides* ..	±	++G	++	++	++	+
5. *M. sylvaticus*	+W	+	+	+	+	+
6. *O. lactis var. A.* ...	—	—	—	—	—	—
7. *O. lactis var. B.* ...	—	—	—	—	—	—
8. *P. biforme*	—*	+G	+	+	+	+
9. *P. expansum*	—*	+G	+	+	+	+
10. *R. nigricans*	+W	+	+	+	+	+
Check	—	—	—	—	—	—

* Roquefort odor.

f. Old Butterfat Plus Water

Methods. The procedure was the same as that just described under "e" except that the old butterfat prepared for experiment "b" was employed.

Results. The growth of the molds on old butterfat was increased when water was present, as the data in Table VII indicate. The development of Cultures 1, 3, and 4 was particularly good. Cultures 6 and 7 failed to grow. It may be noted that the Roquefort cheese odor, which appeared in the fresh butterfat with water in the case of Cultures 8 and 9, was not evident in the old butterfat-water mixture.

TABLE VII

GROWTH OF MOLD CULTURES ON A MIXTURE OF 1.5 PER CENT WASHED AGAR AND OLD BUTTERFAT

(4 parts of agar medium: 1 part of butterfat)

Culture	Extent of growth at 20-25° C., ordinary humidity, after					
	4 days	1 week	2 weeks	3 weeks	4 weeks	4 weeks
	Visible					Microscopic
1. *Alt. humicola*	+W	+	++G	++	++	+
2. *A. flavus*	—	—	+YG	+	+	+
3. *A. niger*	+B	++	++	++	++	+
4. *H. cladosporioides* ..	±	++G	++	++	++	+
5. *M. sylvaticus*	+W	+	+	+	+	+
6. *O. lactis var. A.* ...	—	—	—	—	—	—
7. *O. lactis var. B.* ...	—	—	—	—	—	—
8. *P. biforme*	—	—	+G	+	+	+
9. *P. expansum*	—	—	+G	+	+	+
10. *R. nigricans*	+W	+	+	+	+	+
Check	—	—	—	—	—	—

g. Alcohol-Extracted Butterfat Plus Water

Methods. The method of preparing the substrate was the same as that described in "e" except that the butterfat washed with alcohol (see experiment "d") was used. The methods of inoculation and incubation were the same as those followed in experiment "e."

Results. The growth of Cultures 1, 2, 3, and 4 was quite extensive, as shown in Table VIII. As before, Cultures 6 and 7 showed no signs of development. The Roquefort cheese odor was apparent in Culture 8 at the end of 4 days. In general, the growth was practically the same as when water was added to the fresh and old butterfats.

TABLE VIII

GROWTH OF MOLD CULTURES ON A MIXTURE OF 1.5 PER CENT WASHED AGAR AND ALCOHOL-WASHED BUTTERFAT

(4 parts of agar medium: 1 part of butterfat)

Culture	Extent of growth at 20-25° C., ordinary humidity, after					
	4 days	1 week	2 weeks	3 weeks	4 weeks	4 weeks
	Visible					Microscopic
1. *Alt. humicola*	+W	+	++G	++	++	+
2. *A. flavus*	+Y	++YG	++	++	++	+
3. *A. niger*	+B	++	++	++	++	+
4. *H. cladosporioides* ..	±	++G	++	++	++	+
5. *M. sylvaticus*	+W	+	+	+	+	+
6. *O. lactis var. A.* ...	—	—	—	—	—	—
7. *O. lactis var. B.* ...	—	—	—	—	—	—
8. *P. biforme*	—*	+G	+	+	+	+
9. *P. expansum*	—	+G	+	+	+	+
10. *R. nigricans*	+W	+	+	+	+	+
Check	—	—	—	—	—	—

* Roquefort odor.

h. One-half Per Cent Aqueous Emulsion of Milk Lecithin

Methods. A highly purified lecithin obtained from milk by Dr. W. E. Petersen and Dr. L. M. Thurston, of the Minnesota Agricultural Experiment Station, was emulsified by thoro shaking in water. It produced a stable, milky emulsion, which was tubed and autoclaved. After sterilization, a flocculent precipitate was formed but it remained uniformly suspended after cooling. The emulsion was inoculated from the various cultures and left at room temperature (20° to 25° C.) for 3 weeks, at a relative humidity of 60 to 65 per cent.

TABLE IX

Growth of Mold Cultures in 1.5 Per Cent Aqueous Solution of Milk Lecithin

Culture	Extent of growth at 20–25° C., ordinary humidity, after			
	3 days	1 week	2 weeks	3 weeks
1. *Alt. humicola*	—	—	+W(++)*	++(++)
2. *A. flavus*	—	—	+W(+)	++YG(+)
3. *A. niger*	+WB	+	+(+)	+B(+)
4. *H. cladosporioides* ..	—	—	+G(+)	+(+)
5. *M. sylvaticus*	—	—	—(+)	—(+)
6. *O. lactis var. A.* ...	—	—	—(+)	—(+)
7. *O. lactis var. B.* ...	—	—	—(+)	—(+)
8. *P. biforme*	—	++G	++(+)	++(+)
9. *P. expansum*	—	—	+W(+)	+(+)
10. *R. nigricans*	—	—	—(+)	—(+)
Check	—	—	—	—

* Signs in parentheses indicate subsurface growth.

Results. Table IX gives the results obtained with this emulsion of lecithin. With Culture 3, a white mycelium and a few black sporangia appeared on the walls of the tube just above the surface of the liquid after 3 days. Culture 8 produced a good, green surface growth at the end of one week. Cultures 1, 2, and 9 produced white rings near the surface of the solution after 2 weeks, but at the end of 3 weeks were growing reasonably well on the surface. All cultures showed subsurface mycelial development, which was especially good in Culture 10. Unquestionably lecithin was a fairly good source of food for these species.

i. One-half Per Cent Aqueous Emulsion of Milk Lecithin in 1.5 Per Cent Washed Agar

Methods. A portion of the sterile lecithin emulsion, prepared according to the methods described in the preceding trial, was added to an equal amount of melted, sterile, 1.5 per cent washed agar made up in 5-cc. amounts in test tubes. After thoro mixing, the medium was slanted. The agar slants were inoculated over the surface in the usual manner. The tubes were incubated at room temperature (20° to 25° C.) for 3 weeks at a relative humidity of 60 to 65 per cent.

Results. It will be noted in Table X that growth began promptly in all cases, and became practically normal after 3 weeks with the exception of Cultures 6 and 7, which already had been shown to do very poorly on fat or fat-like substrata. The development of the cultures was much better on the solid medium than on the fluid preparation.

TABLE X

GROWTH OF MOLD CULTURES ON MIXTURE OF 1.0 PER CENT WASHED AGAR AND 0.5 PER CENT AQUEOUS SOLUTION OF MILK LECITHIN

(Equal parts of agar medium and lecithin solution)

Culture	Extent of growth at 20–25° C., ordinary humidity, after			
	3 days	1 week	2 weeks	3 weeks
1. *Alt. humicola*	++W	+++G	+++	+++
2. *A. flavus*	+W	++Y	++YG	++
3. *A. niger*	+W	+W	+B	++
4. *H. cladosporioides* ..	+W	++G	+++G	+++
5. *M. sylvaticus*	++W	+++	+++WB	+++
6. *O. lactis var. A.* ...	+W	+	+	+
7. *O. lactis var. B.* ...	+W	+	+	+
8. *P. biforme*	+W	+	+G	++
9. *P. expansum*	+W	+	+++G	+++
10. *R. nigricans*	++W	+++	+++WB	+++
Check	—	—	—	—

j. One Per Cent Glycerol in 1.5 Per Cent Washed Agar

Methods. Chemically pure glycerol was added to melted, sterile, 1.5 per cent washed agar in amount sufficient to make a one per cent solution. This mixture was tubed, autoclaved, and slanted. The usual agar stroke was made with each culture. The cultures were then placed in a humidor, which consisted of a covered 10-gallon metal churn, equipped with a false, perforated bottom, under which was placed a quantity of water to which bichloride of mercury had been added to maintain sterility. The relative humidity was maintained at 100 per cent. The temperature of incubation was 20° to 25° C. and the storage period 3 weeks.

TABLE XI

GROWTH OF MOLD CULTURES ON 1.5 PER CENT WASHED AGAR CONTAINING 1 PER CENT GLYCEROL

Culture	Extent of growth at 20–25° C., high humidity, after			
	3 days	1 week	2 weeks	3 weeks
1. *Alt. humicola*	±	+W(++)	+(+++G)	+(+++)
2. *A. flavus*	+W(+)	+G(++)	+(++)	++(+++)
3. *A. niger*	±	+B(+)	+(+)	+(++)
4. *H. cladosporioides* ..	±(+G)	+G(++)	+(+++)	+(+++)
5. *M. sylvaticus*	±(++)	+W(++)	+(++)	+(++)
6. *O. lactis var. A.* ...	+W(++)	+(++)	+(+++)	+(+++)
7. *O. lactis var. B.* ...	+W(++)	+(++)	+(+++)	+(+++)
8. *P. biforme*	±	+G(+)	+(+)	+(+)
9. *P. expansum*	±(+)	+G(++)	+(+++)	+(+++)
10. *R. nigricans*	±W(+)	+(+)	+(+)	+WB(+)
Check	—	—	—	—

Results. Table XI gives the results of this experiment. It will be observed that Cultures 2, 6, 7, and 10 showed some growth after 3 days. With the rest, growth became noticeable after one week. However, none of the cultures exhibited any further surface growth except Culture 2, which had developed extensively after 3 weeks. The significant result was the extensive subsurface growth of nearly all cultures. This subsurface development in most cases was much more marked than the surface growth. Cultures 1 and 4 produced remarkable dark green subsurface mycelium. The same phenomenon appeared in aqueous solutions of glycerol, studied in preliminary unreported trials.

k. One Per Cent Butyric Acid in 1.5 Per Cent Washed Agar

Methods. Purified butyric acid was added to measured amounts of tubed, melted, sterile, 1.5 per cent washed agar medium in quantities sufficient to make a one per cent solution. These tubes were shaken thoroly and slanted. After inoculation the cultures were placed in a metal humidor (described previously) at 20° to 25° C. for 3 weeks, and at a relative humidity of 100 per cent.

TABLE XII

GROWTH OF MOLD CULTURES ON 1.5 PER CENT WASHED AGAR CONTAINING 1 PER CENT BUTYRIC ACID

Culture	Extent of growth at 20–25° C., high humidity, after			
	3 days	1 week	2 weeks	3 weeks
1. *Alt. humicola*	—	—	—	—
2. *A. flavus*	—	—	—	—
3. *A. niger*	—	—	—	—
4. *H. cladosporioides* ..	—	—	—	—
5. *M. sylvaticus*	—	—	—	—
6. *O. lactis var. A.* ...	—	—	—	—
7. *O. lactis var. B.* ...	—	—	—	—
8. *P. biforme*	—	—	—	—
9. *P. expansum*	—	—	—	—
10. *R. nigricans*	—	—	—	—
Check	—	—	—	—

Results. Table XII reveals the fact that the cultures under investigation were unable to develop in this concentration of butyric acid. This is in agreement with the results of preliminary studies.

l. One Per Cent Palmitic Acid in 1.5 Per Cent Washed Agar

Methods. Purified palmitic acid was added in a sufficient quantity to a sterile, melted, 1.5 per cent washed agar medium to make a one per cent concentration. After warming the mixture in a steam bath until the palmitic acid melted, it was shaken thoroly and placed as quickly as possible in sterile tubes. The tubes were rotated thoroly so that the acid was fairly well dispersed and the medium solidified as quickly as possible in a slanted position. The acid hardened on the surface in areas ranging from 0.1 mm. to 5.0 mm. in diameter, with equal areas of clear agar between them, while the bulk of the medium was clear. The inoculations were made over the surface in such a way that the cultures covered representative areas of the solidified acid.

The tubes were incubated under the conditions prevailing in the previous experiment.

Results. The growth on the medium containing palmitic acid as the source of nutriment was fairly good, as shown in Table XIII. All cultures exhibited some surface growth, which was much better than that obtained on the agar checks. The remarkable feature of this series, however, was the extensive development of Cultures 1, 2, 4, 5, 6, and 10 below the surface. The mycelium grew directly away from the surface of the slants and in Cultures 1 and 4, the hyphae were dark green.

TABLE XIII

GROWTH OF MOLD CULTURES ON 1.5 PER CENT WASHED AGAR CONTAINING 1 PER CENT PALMITIC ACID

	Extent of growth at 20–25° C., high humidity, after			
Culture	3 days	1 week	2 weeks	3 weeks
1. *Alt. humicola*	+W(++G)	+G(++)	+(++)	+(++)
2. *A. flavus*	+W(++)	+YG(++)	+(++)	+(++)
3. *A. niger*	+W(+)	+B(+)	+(+)	+(+)
4. *H. cladosporioides* ..	+W(+)	+G(++G)	+(++)	+(++)
5. *M. sylvaticus*	+W(++)	+(++)	++(++)	++(++)
6. *O. lactis var. A.* ...	—(+)	+W(+)	+(++)	+(++)
7. *O. lactis var. B.* ...	—(+)	+(+)	+(+)	+(+)
8. *P. biforme*	—	+G(+)	+(+)	+(+)
9. *P. expansum*	—	+G(+)	+(+)	+(+)
10. *R. nigricans*	+W(++)	++(++)	++WB(++)	++(++)
Check	—	—	—	—

m. One Per Cent Stearic Acid in 1.5 Per Cent Washed Agar

Methods. The one per cent concentration of stearic acid in 1.5 per cent washed agar substrate was prepared in the same manner as the preceding mixture of palmitic acid and agar. The emulsion obtained in this case, however, was more uniform. The medium became very cloudy. Inoculation and incubation conditions were identical with the foregoing "k" and "l."

TABLE XIV

GROWTH OF MOLD CULTURES ON 1.5 PER CENT WASHED AGAR CONTAINING 1 PER CENT STEARIC ACID

	Extent of growth at 20–25° C., high humidity, after			
Culture	3 days	1 week	2 weeks	3 weeks
1. *Alt. humicola*	+W	+W	+WG	+G
2. *A. flavus*	—	—	—	—
3. *A. niger*	—	—	—	—
4. *H. cladosporioides* ..	—	—	—	—
5. *M. sylvaticus*	—	—	—	—
6. *O. lactis var. A.* ...	—	—	—	—
7. *O. lactis var. B.* ...	—	—	—	—
8. *P. biforme*	—	—	—	—
9. *P. expansum*	—	—	—	—
10. *R. nigricans*	—	—	—	—
Check	—	—	—	—

Results. Table XIV gives the results of this experiment. The only surface development observed in this medium occurred with Culture 1, where a small area of growth appeared about the point of inoculation. The medium was so opaque that it was impossible to determine whether any subsurface growth had taken place.

n. One Per Cent Oleic Acid in 1.5 Per Cent Washed Agar

Methods. Purified oleic acid was measured into definite amounts of sterile, melted, 1.5 per cent washed agar medium in tubes so that the concentration of acid was one per cent. The mixture was shaken thoroly and solidified as quickly as possible in a slanting position. The oleic acid appeared in the surface in clear droplets, approximately one mm. in diameter and close together. Conditions of inoculation and incubation were exactly the same as in the three preceding trials.

TABLE XV

GROWTH OF MOLD CULTURES ON 1.5 PER CENT WASHED AGAR CONTAINING 1 PER CENT OLEIC ACID

Culture	Extent of growth at 20–25° C., high humidity, after			
	3 days	1 week	2 weeks	3 weeks
1. *Alt. humicola*	+W(++)	++WG(++G)	++(++)	++(++)
2. *A. flavus*	+G(++)	++(+++)	++(+++)	++(+++)
3. *A. niger*	−(+)	+B(++)	+(++)	+(+++)
4. *H. cladosporioides*	+G(++)	++B(++G)	++(+++)	++(+++)
5. *M. sylvaticus*	+W(++)	++(++)	++(++)	++(++)
6. *O. lactis var. A.*	−(+)	+W(++)	+(++)	+(++)
7. *O. lactis var. B.*	−(+)	+W(++)	+(+++)	+(+++)
8. *P. biforme*	−(+)	+G(++)	+(++)	+(++)
9. *P. expansum*	−(+)	+G(++)	++(+++)	++(+++)
10. *R. nigricans*	+W(++)	++(++)	++WB(++)	++(++)
Check	—	—	—	—

Results. As indicated in Table XV the growth on this substrate was better than that obtained on media containing any of the other acids commonly found in butterfat. Surface development was good in all except Cultures 3, 6, 7, and 8. The subsurface mycelium was remarkably heavy, especially in Cultures 2, 3, 4, 7, and 9. Cultures 1 and 4 produced their characteristic dark green hyphae in the depth of the medium.

2. Proteins and Related Substances

a. One Per Cent Aqueous Solution of Peptone

Methods. A one per cent solution of Bacto peptone was prepared in distilled water, tubed, and autoclaved. The peptone solution was inoculated in the usual manner with each of the cultures. The tubes were incubated under conditions identical with those employed in the preceding experiment.

Results. The growth of the cultures began promptly in this solution as indicated in Table XVI. At the end of one week, the development of all cultures was good, and in some cases perfectly normal. While some subsurface development was noted, it was not nearly so extensive as that on the surface.

TABLE XVI

GROWTH OF MOLD CULTURES ON 1 PER CENT AQUEOUS SOLUTION OF PEPTONE (BACTO)

Culture	Extent of growth at 20–25° C., high humidity, after			
	3 days	1 week	2 weeks	3 weeks
1. *Alt. humicola* ……	+W(++)	++WG(+)	++WG	++G
2. *A. flavus* ……….	++W	++WY	+++YBr	++++Br
3. *A. niger* ……….	++W(+)	+++B(+)	++++(+)	++++(+)
4. *H. cladosporioides* ..	++G(+)	+++(+)	++++(+)	++++(+)
5. *M. sylvaticus* ……	++W(++)	+++(+)	+++(+)	++++(+)
6. *O. lactis var. A.* …	+++W(++)	++++(++)	++++(++)	++++(++)
7. *O. lactis var. B.* …	++W(++)	+++(++)	++++(++)	++++(++)
8. *P. biforme* ……..	++G(+)	+++(+)	++++(+)	++++(+)
9. *P. expansum* …….	++W(+)	++++	++++	++++
10. *R. nigricans* …….	+++W(++)	++++(+)	++++(+)	++++WB(+)
Check ………….	—	—	—	—

b. "Curd" Portion of Butter

Methods. Fresh, unsalted butter was melted at 60° to 65° C. and placed in a warm separatory funnel from which the so-called "curd" was withdrawn with ease, as it settled below the melted fat. This curd, which consisted principally of protein, was tubed and autoclaved. The water content was 86.3 per cent. The curd was inoculated with the test cultures. The tubes were placed in a humidor (as described under the preparation of fresh butterfat), where the relative humidity remained at 100 per cent during the storage period. The temperature of incubation was 20° to 25° C.

TABLE XVII

GROWTH OF MOLD CULTURES ON CURD PORTION OF BUTTER

Culture	Extent of growth at 20–25° C., high humidity, after			
	2 days	4 days	1 week	2 weeks
1. *Alt. humicola* ……	—	++++G	++++	++++
2. *A. flavus* ……….	++W	+++YG	++++	++++
3. *A. niger* ……….	+B	+++	++++	++++
4. *H. cladosporioides* …	++G	++++	++++	++++
5. *M. sylvaticus* ……	+++WB	++++	++++	++++
6. *O. lactis var. A* …	++W	++	+++	++++
7. *O lactis var. B.* …	+W	+++C	++++	++++
8. *P. biforme* ……..	—	++++G	++++	++++
9. *P. expansum* …….	+G	++++	++++	++++
10. *R. nigricans* …….	+++WB	++++	++++	++++
Check ………….	—	—	—	—

Results. The growth of all cultures, except Cultures 1 and 8, became visible within 4 days, as is shown in Table XVII. At the end of one week, development was practically normal. The growth reached a maximum after 2 weeks and further incubation resulted in no noticeable changes. It will be noted that growth was both rapid and luxuriant.

c. Dialyzed Curd from Butter

Methods. A portion of the curd obtained by the method outlined in the previous experiment was placed in a collodion sac and dialyzed in distilled water for 24 hours. It was then tubed and autoclaved. The final preparation contained 89.3 per cent water. The conditions of inoculation and incubation were identical with those employed in the previous trial.

TABLE XVIII

Growth of Mold Cultures on Dialyzed Curd from Butter

	Extent of growth at 20–25° C., high humidity, after			
Culture	2 days	4 days	1 week	2 weeks
1. *Alt. humicola*	—	+++G	++++	++++
2. *A. flavus*	+W	+++YG	+++	+++
3. *A. niger*	+W	++++B	++++	++++
4. *H. cladosporioides* ..	+++G	++++	++++	++++
5. *M. sylvaticus*	++W	++++WB	++++	++++
6. *O. lactis var. A.* ...	+W	++	+++	+++
7. *O. lactis var. B.* ...	+W	++	+++	+++
8. *P. biforme*	—	+++G	++++	++++
9. *P. expansum*	—	+++G	+++	+++
10. *R. nigricans*	+W	+++WB	++++	++++
Check	—	—	—	—

Results. The growth of the molds did not begin as promptly as it did on normal curd preparations, as indicated in Table XVIII. After 4 days, however, the growth was marked and after one week it reached a maximum. In general, the development was not quite so vigorous as that observed on untreated curd.

d. Washings from Cream

Methods. The sera (obtained from the successive washings of cream as explained in a previous experiment) were collected after each separation, tubed, and autoclaved. The first, third, sixth, and tenth rinsings were selected for this purpose. The first washing appeared quite milky, resembling diluted skimmilk. The tenth washing was practically clear. The washings were inoculated in the usual manner with the various cultures. The tubes were kept at 20° to 25° C. for one week, at a relative humidity of 60 to 65 per cent.

Results. Table XIX gives the results obtained when the washings were inoculated with the test cultures. Growth was practically normal in the serum from the first washing after one week, with the exception of Cultures 6 and 7. In the third washings, Cultures 1, 8, and 9 were the only ones to show any development and this was rather scanty. Culture 1 was able to grow on the sixth and tenth washings; none of the others produced any visible growth with the exception of a slight development of Culture 8 on the tenth washing. It was apparent that most of the nutrients must have been removed from the cream by the early washings.

TABLE XIX

GROWTH OF MOLD CULTURES ON WASHINGS FROM CREAM

Culture	Extent of growth at 20–25° C., ordinary humidity							
	1st washing		3rd washing*		6th washing*		10th washing*	
	3 days	1 week	3 days	1 week	3 days	1 week	3 days	1 week
1. *Alt. humicola*	++++G	++++	+	++	+	+	+	+
2. *A. flavus*	++Y	++++	—	—	—	—	—	—
3. *A. niger*	—	++B	—	—	—	—	—	—
4. *H. cladosporioides*	++++G	++++	—	—	—	—	—	—
5. *M. sylvaticus*	+++W	+++	—	—	—	—	—	—
6. *O. lactis var. A.*	—	+W	—	—	—	—	—	—
7. *O. lactis var. B.*	+W	+	—	—	—	—	—	—
8. *P. biforme*	+++G	++++	+G	+	—	—	—	+G
9. *P. expansum*	+G	++++	+G	+	—	—	—	—
10. *R. nigricans*	++W	++++	—	—	—	—	—	—
Check	—	—	—	—	—	—	—	—

* All cultures on 3rd, 6th, and 10th washings showed slight subsurface growth.

3. Carbohydrates and Related Substances

a. One Per Cent Aqueous Solution of Lactose

Methods. A one per cent aqueous solution of chemically pure lactose was prepared in distilled water, tubed, and autoclaved. The tubes were inoculated in the usual manner and kept for 3 weeks at a temperature of 20° to 25° C. and a relative humidity of 100 per cent, in the metal humidor previously described.

TABLE XX

GROWTH OF MOLD CULTURES ON 1 PER CENT AQUEOUS SOLUTION OF LACTOSE

Culture	Extent of growth at 20-25° C., high humidity, after			
	3 days	1 week	2 weeks	3 weeks
1. *Alt. humicola*	—(+)	+W(+)	++G(++G)	++(++)
2. *A. flavus*	—(+)	+W(+)	+(+)	+(+)
3. *A. niger*	—(+)	+W(+)	+(+)	+(+)
4. *H. cladosporioides*	—	—	+G	+(+)
5. *M. sylvaticus*	—(+)	+W(+)	+(+)	+(+)
6. *O. lactis var. A.*	—(+)	—(+)	—(+)	+W(+)
7. *O. lactis var. B.*	—	—(+)	—(+)	+W(+)
8. *P. biforme*	—(+)	+W(+)	+(+)	++WG(++)
9. *P. expansum*	—(+)	+W(+)	+(+)	+(+)
10. *R. nigricans*	—(+)	+W(+)	+(++)	+(++)
Check	—	—	—	—

Results. Table XX indicates that the only signs of growth after 3 days incubation took place in the depth of the liquid or downward from the surface, where the conidia floated. At the end of one week, feeble surface growth was noted except with Cultures 6 and 7. The subsurface development was somewhat more extensive. After 3 weeks, Cultures 1 and 8 had sent up considerable mycelium from the surface, but at the same time the subsurface growth was equally good. In general, the development in the lactose solution was not marked at any time.

b. One Per Cent Aqueous Solution of Lactose in 1.5 Per Cent Washed Agar

Methods. One gram of chemically pure lactose was added to 100 cc. of 1.5 per cent washed agar, and the mixture was tubed, autoclaved, and slanted. The usual inoculations were made and the tubes incubated under conditions described in the previous trial.

TABLE XXI

Growth of Mold Cultures on 1.5 Per Cent Washed Agar Containing 1 Per Cent Lactose

Culture	Extent of growth at 20–25° C., high humidity, after			
	3 days	1 week	2 weeks	3 weeks
1. *Alt. humicola*	−(+)	+W(++)	+(+++G)	+(+++)
2. *A. flavus*	+W(+)	+YG(++)	+(++)	+(+++)
3. *A. niger*	+W(+)	+B(+)	+(++)	+(++)
4. *H. cladosporioides* ..	+G(++G)	+(++)	+(+++)	+(+++)
5. *M. sylvaticus*	+W(++)	+(++)	+(++)	+(++)
6. *O. lactis var. A.* ...	+W(++)	+(++)	+(++)	+(++)
7. *O. lactis var. B.* ...	+W(++)	+(++)	+(++)	+(++)
8. *P. biforme*	+G(++)	+(++)	+(+++)	+(+++)
9. *P. expansum*	+G(+)	+(++)	+(+++)	+(+++)
10. *R. nigricans*	+W(+)	+(+)	+(+)	+(+)
Check	−	−	−	−

Results. The surface growth was slight, even after 3 weeks incubation, as shown in Table XXI. Subsurface development in most cases was marked. Cultures 1 and 4 produced dark green mycelium that penetrated deep into the solid medium, at right angles with the side walls of the tube. This is illustrated plainly in Plates I and II. The growth resembled that obtained on solid media containing glycerol.

c. One Per Cent Lactic Acid in 1.5 Per Cent Washed Agar

Methods. Purified lactic acid was added to measured quantities of sterile, melted, 1.5 per cent washed agar in tubes, in amounts sufficient

TABLE XXII

Growth of Mold Cultures on 1.5 Per Cent Washed Agar Containing 1 Per Cent Lactic Acid

Culture	Extent of growth at 20–25° C., high humidity, after			
	3 days	1 week	2 weeks	3 weeks
1. *Alt. humicola*	−	−	+G	+G
2. *A. flavus*	+W(+)	+(+)	+Y(+)	+YG(+)
3. *A. niger*	+W(+)	+B(++)	++(++)	++(++)
4. *H. cladosporioides* ..	−	+G	++(+)	++(+G)
5. *M. sylvaticus*	−	−	−	−
6. *O. lactis var. A*	−	−	−	−
7. *O. lactis var. B.* ...	−	−	−	−
8. *P. biforme*	+G(+)	+(++)	+(++)	+(++)
9. *P. expansum*	−	+W(+)	+G(+)	+(+)
10. *R. nigricans*	−	+W	+	+
Check	−	−	−	−

to make a one per cent solution. After thoro mixing the tubes were slanted. The slants were inoculated in the usual manner and incubated at 20° to 25° C. for 3 weeks in a metal humidor (described elsewhere), in which the relative humidity was maintained at 100 per cent.

Results. The results of this trial are given in Table XXII. It will be noted that Cultures 3 and 4 made moderate, Cultures 1, 2, 8, 9, and 10 slight, and Cultures 5, 6, and 7 no growth in this medium. The subsurface development was particularly good in Cultures 3 and 8. Cultures 4 sent dark green hyphae into the depth of the medium. Where growth appeared, it was better than that obtained on the pure agar substrate.

d. Diffusate from Curd of Butter

Methods. The diffusate obtained in the dialysis of the curd from butter, as explained in previous pages, was tubed and autoclaved. The diffusate contained 99.7 per cent of water and 0.00238 per cent of nitrogen at the time of inoculation. It was inoculated and kept at 20° to 25° C. for 3 weeks in a humidor at a relative humidity of 100 per cent.

TABLE XXIII

Growth of Mold Cultures on Diffusate from Curd of Butter

Culture	Extent of growth at 20-25° C., high humidity, after				
	2 days	4 days	1 week	2 weeks	3 weeks
1. *Alt. humicola*	++W	+++	+++	+++	++++G
2. *A. flavus*	++Y	++YG	++	++	++
3. *A. niger*	+B	+	+	+	+
4. *H. cladosporioides* ..	++G	++	++	++	++
5. *M. sylvaticus*	+W	+	+	+	+
6. *O. lactis var. A.* ...	+W	+	+	+	+
7. *O. lactis var. B.*	—	—	—	+W	+
8. *P. biforme*	++G	++	++	++	++
9. *P. expansum*	+G	++	++	++	++
10. *R. nigricans*	+W	+	+	+	+++
Check	—	—	—	—	-

Results. Table XXIII gives the results of this experiment. It will be noted that growth began promptly except with Culture 7, which did not produce visible mycelium until the second week. Cultures 2, 3, 5, 6, 8 and 9 reached the point of maximum development after 4 days. The growth of Cultures 1, 4, and 10 became especially luxuriant. Apparently, the food materials were readily available, as evidenced by the prompt growth, but were so rapidly utilized by certain of the cultures that development reached an early maximum.

4. Mineral Constituents

a. Milk Ash in 0.75 Per Cent Aqueous Solution

Methods. One pint of fresh skimmilk was evaporated to dryness over a water bath, the residue incinerated in a muffle furnace, and the ash recovered. A 0.75 per cent aqueous solution was prepared, tubed, and autoclaved. The inoculated tubes were incubated at 20° to 25° C. for 2 weeks, at a relative humidity of 60 to 65 per cent. At the end of 2 weeks, one cc. of sterile skimmilk was added to each tube to determine whether the cultures were in a viable condition.

TABLE XXIV

GROWTH OF MOLD CULTURES ON 0.75 PER CENT AQUEOUS SOLUTION OF MILK ASH

Culture	Extent of growth at 20–25° C., ordinary humidity, after			Growth 3 days after adding 1 cc. sterile skimmilk
	4 days	1 week	2 weeks	
1. *Alt. humicola*	−	−	−	+++G
2. *A. flavus*	+	+	+	++YG
3. *A. niger*	−	−	−	+B
4. *H. cladosporioides* ..	−	−	−	+++B
5. *M. sylvaticus*	−	−	−	++W
6. *O. lactis var. A.* ...	−	−	−	++W
7. *O. lactis var. B.* ...	−	−	−	+W
8. *P. biforme*	−	−	−	+++G
9. *P. expansum*	−	−	−	+++G
10. *R. nigricans*	−(+)	−(+)	−(+)	+++W
Check	−	−	−	−

Results. As shown in Table XXIV, no growth occurred with most of the cultures. There was a slight subsurface mycelium in Culture 10, and a barely visible development in Culture 2. Three days after the sterile skimmilk was added, excellent growth was obtained from all except Cultures 2 and 7.

b. Milk Ash in 0.75 Per Cent Aqueous Solution Neutralized with Hydrochloric Acid

Methods. The solution of milk ash, prepared according to the method outlined in the foregoing experiment, was neutralized with hydrochloric acid. The methods of tubing, sterilizing, and inoculating, and the conditions of incubation were identical with those followed in the previous trial.

TABLE XXV

GROWTH OF MOLD CULTURES ON 0.75 PER CENT AQUEOUS SOLUTION OF MILK ASH MADE NEUTRAL WITH HYDROCHLORIC ACID

Culture	Extent of growth at 20–25° C., ordinary humidity, after			Growth 3 days after adding 1 cc. sterile skimmilk
	4 days	1 week	2 weeks	
1. *Alt. humicola*	++W	++	++	+++WG
2. *A. flavus*	+W	+	+	++WY
3. *A. niger*	+WB	+	+	++B
4. *H. cladosporioides* ..	−	+W	+	++G
5. *M. sylvaticus*	−	−(+)	−(+)	++W
6. *O. lactis var. A.* ...	−	−	−	+++W
7. *O. lactis var. B.* ..	−	−	−	+W
8. *P. biforme*	++W	++	++	+++G
9. *P. expansum*	++W	++	++	+++G
10. *R. nigricans*	−(+)	−(+)	−(+)	+++W
Check	−	−	−	−

Results. It will be noted from Table XXV that fairly good growth took place after 4 days in Cultures 1, 8, and 9, while Cultures 2 and 3 showed scanty mycelial development. At the end of 2 weeks all cultures except 6 and 7 exhibited some degree of growth. Cultures 5 and 10, however, produced only subsurface mycelium. The addition of sterile milk showed that none of the cultures had been killed; all grew well in 3 days, with Culture 7 again the least active.

5. Combinations of Various Foodstuffs

a. Emulsion of Butterfat, Milk Lecithin, and Water

Methods. Five parts of old, sterile butterfat, prepared according to the methods described on page 23, were mixed thoroly with one part of a one per cent sterile aqueous emulsion of lecithin, and the mixture was poured into petri plates. These plates were inoculated by streaking the cultures across the surface, and were incubated at 20° to 25° C. for 3 weeks at a relative humidity of 100 per cent in the earthenware humidor previously described.

TABLE XXVI

Growth of Mold Cultures on Emulsion of Butterfat and One Per Cent Aqueous Solution of Milk Lecithin

(5 parts of butterfat: 1 part of lecithin solution)

Culture	Extent of growth at 20–25° C., high humidity, after			
	3 days	1 week	2 weeks	3 weeks
1. *Alt. humicola*	+W	+	+	++
2. *A. flavus*	—	—	—	—
3. *A. niger*	—	—	—	+B
4. *H. cladosporioides* ..	—	—	—	+G
5. *M. sylvaticus*	—	—	—	—
6. *O. lactis var. A.* ...	—	—	—	—
7. *O. lactis var. B.* ...	—	—	—	—
8. *P. biforme*	—	—	—	—
9. *P. expansum*	—	—	—	—
10. *R. nigricans*	—	—	—	—
Check	—	—	—	—

Results. The growth on the mixture of butterfat, lecithin, and water was not much better than that obtained on fat alone, as is clearly demonstrated in Table XXVI. Culture 1 began its development promptly and showed the best growth. Cultures 3 and 4 produced a scanty but visible surface growth.

b. Butterfat Plus Dry Milk Ash

Methods. Some of the old butterfat used in previous experiments was melted, poured into petri plates, and solidified promptly. Dry milk ash was sprinkled freely over the surface. The cultures were streaked across the surface in such a way that they came into contact both with the ash and the fat. The plates were incubated for 3 weeks in the earthenware humidor at a temperature of 20° to 25° C. and a relative humidity of 100 per cent.

Results. Table XXVII gives the results obtained. The growth was somewhat better than that on pure butterfat. Visible mycelium was observed in Cultures 1, 2, 3, 4, 8, and 9 after 3 weeks incubation. Cultures 5, 6, and 7 showed no signs of development when the plates were examined under the microscope; Culture 10 gave evidence of the germination of some of the conidia and abortive mycelium.

TABLE XXVII

GROWTH OF MOLD CULTURES ON BUTTERFAT WITH MILK ASH SPRINKLED OVER SURFACE

Culture	Extent of growth at 20–25° C., high humidity, after			
	1 week	2 weeks	3 weeks	3 weeks
	Visible			Microscopic
1. *Alt. humicola*	+W	+G	++G	+
2. *A. flavus*	—	+YG	+	+
3. *A. niger*	++B	++	++	+
4. *H. cladosporioides* ..	—	—	++G	+
5. *M. sylvaticus*	—	—	—	—
6. *O. lactis var. A.* ...	—	—	—	—
7. *O. lactis var. B.* ...	—	—	—	—
8. *P. biforme*	—	—	+G	+
9. *P. expansum*	—	—	+G	+
10. *R. nigricans*	—	—	—	+
Check	—	—	—	—

c. Mixture of Butterfat, Milk Ash, and Water

Methods. Two parts of sterile fresh butterfat and one part of milk ash (prepared in accordance with methods described on page 39) were mixed thoroly and added to four parts of a sterile, melted, 1.5 per cent washed agar medium. The mixture was shaken thoroly and poured into petri plates. After it had become hard, the cultures were streaked across the surface. The plates were incubated for 4 weeks at a temperature of 20° to 25° C. and a relative humidity of 60 to 65 per cent.

TABLE XXVIII

GROWTH OF MOLD CULTURES ON 1.5 PER CENT WASHED AGAR WITH FRESH BUTTERFAT AND SATURATED SOLUTION OF MILK ASH ADDED

(4 parts of agar medium: 2 parts of butterfat and 1 part of ash solution)

Culture	Extent of growth at 20–25° C., ordinary humidity, after					
	4 days	1 week	2 weeks	3 weeks	4 weeks	4 weeks
	Visible					Microscopic
1. *Alt. humicola*	+W	+G	+	++	++	+
2. *A. flavus*	+Y	++	++YG	++	++	+
3. *A. niger*	+B	++	++	++	++	+
4. *H. cladosporioides* ..	+G	++	++	++	++	+
5. *M. sylvaticus*	+W	+	+	+	+	+
6. *O. lactis var. A.* ...	—	—	—	—	—	—
7. *O. lactis var. B.* ...	—	—	—	—	—	—
8. *P. biforme*	+W	+	+G	+	+	+
9. *P. expansum*	+W	+G	+	+	+	+
10. *R. nigricans*	+W	+	+	+	+	+
Check	—	—	—	—	—	—

Results. Table XXVIII indicates that growth began within a few days and increased slightly during the 4 weeks, with the exception of Cultures 6 and 7. Cultures 1, 2, 3, and 4 made the most noticeable progress in this medium. The microscopic examination failed to show any signs of germination of the conidia from Cultures 6 or 7. The failure of these cultures to grow on fats, minerals, or combinations of the two substances has been a regular phenomenon.

d. Aqueous Solution of Lactose and Peptone

Methods. A solution containing one per cent Bacto peptone and one per cent chemically pure lactose was prepared in distilled water, tubed, and autoclaved. After inoculation the samples were incubated at 20° to 25° C. for 3 weeks in the metal humidor at a humidity of 100 per cent.

TABLE XXIX

GROWTH OF MOLD CULTURES IN AQUEOUS SOLUTION CONTAINING 1 PER CENT LACTOSE AND 1 PER CENT PEPTONE

Culture	Extent of growth at 20–25° C., high humidity, after			
	3 days	1 week	2 weeks	3 weeks
1. *Alt. humicola* ...	+W(+)	+++G(++)	+++(++)	++++(++)
2. *A. flavus*	++W(+)	++	+++YBr	++++
3. *A. niger*	++WB(+)	+++B(+)	++++B(+)	++++(+)
4. *H. cladosporioides*	++G(+)	++++G(+)	++++(+)	++++(+)
5. *M. sylvaticus* ...	++W(++)	+++(++)	+++(+)	++++(+)
6. *O. lactis var. A.*	++W(++)	++++(++)	++++(++)	++++(++++)
7. *O. lactis var. B.*	++W(++)	++++(++)	++++(++)	++++(++)
8. *P. biforme*	++W(+)	++++G(+)	++++(+)	++++(++)
9. *P. expansum* ...	++W(+)	++++(+)	++++(+)	++++(+)
10. *R. nigricans*	+++W(++)	++++WB(++)	++++(+)	++++(+)
Check	—	—	—	—

Results. Table XXIX shows that all the cultures grew rapidly in the medium and soon reached a normal state of development as in peptone alone. The only effect that the lactose seemed to exert was an increase in the amount of subsurface mycelium. The protein appeared to be the more readily utilized substance.

e. Mixture of Lactose and Peptone in 1.5 Per Cent Washed Agar

Methods. Sufficient lactose and peptone were added to a 1.5 per cent washed agar medium to give a one per cent concentration of each. This mixture was tubed, autoclaved, and slanted. The slants were inoculated on the surface in the usual manner. The tubes were incubated under conditions described in the previous experiment.

Results. It will be observed in Table XXX that excellent growth was obtained in this medium. In contrast with the lactose-washed agar medium, the surface growth was predominant, altho some subsurface mycelium was produced. The contrast between the growth on the lactose-peptone-washed agar and the lactose-washed agar is shown clearly in Plates I and III. When lactose was the main source of food, the mycelium of the molds studied seemed preferably to penetrate into the depth of the medium, but when a nitrogen compound, such as peptone, was available at the same time, the growth became characteristically concentrated on the surface.

TABLE XXX

GROWTH OF MOLD CULTURES ON 1.5 PER CENT WASHED AGAR CONTAINING 1 PER CENT LACTOSE AND 1 PER CENT PEPTONE

	Extent of growth at 20–25° C., high humidity, after			
Culture	3 days	1 week	2 weeks	3 weeks
1. *Alt. humicola* ...	+W(+)	++WG(+)	+++(+)	++++G(+)
2. *A. flavus*	++W(+)	+++WGY(+)	+++YG(+)	++++(++)
3. *A. niger*	++B(+)	++++(+)	++++(+)	++++(+)
4. *H. cladosporioides*	+++G(+Br)	++++(+)	++++(+)	++++(+)
5. *M. sylvaticus* ...	+++W(+)	+++(+)	+++(++)	+++(+++)
6. *O. lactis var. A.*	++W(+)	++(+)	++(++)	+++(++)
7. *O. lactis var. B.*	+++W(+)	+++(+)	+++(++)	+++(++)
8. *P. biforme*	++++G(+)	++++(+)	++++(+)	++++(++)
9. *P. expansum* ...	+++W(+)	++++(+)	++++G(++)	++++(++)
10. *R. nigricans*	+++W(+)	++++(++)	+++(++)	+++(++)
Check	—	—	—	—

f. Sterile, Unsalted Butter

Methods. A sample of fresh 30 per cent cream was autoclaved and churned in a sterile Dazey churn, the butter was washed with sterile water and worked with sterile paddles. Small pieces of this butter were transferred to sterile test tubes and allowed to harden over night in the cooler. After inoculation by streaking the cultures along the surface, the tubes were placed in a humidor at a temperature of 20° to 25° C. and a relative humidity of 100 per cent for 3 weeks.

TABLE XXXI

GROWTH OF MOLD CULTURES ON STERILE, UNSALTED BUTTER

	Extent of growth at 20–25° C., high humidity, after			
Culture	4 days	1 week	2 weeks	3 weeks
1. *Alt. humicola*	—	+G	+++	++++
2. *A. flavus*	—	—	+YG	+
3. *A. niger*	+B	++	++	+++
4. *H. cladosporioides* ..	+G	+++	+++	+++
5. *M. sylvaticus*	++W	+++WB	+++	+++
6. *O. lactis var. A.* ...	—	—	—	—
7. *O. lactis var. B.* ...	—	—	—	—
8. *P. biforme*	—	++G	++	+++
9. *P. expansum*	+G	+++	+++	+++
10. *R. nigricans*	—	+W	+++WB	+++
Check	—	—	—	—

Results. The growth of the cultures on this combination of all of the foodstuffs previously studied is described in Table XXXI and illustrated in Plate III. The most extensive development was noted in Cultures 1, 3, 4, 5, 8, 9, and 10. The butter was discolored to the greatest extent with Cultures 1 and 4. Culture 2 showed slight visible mycelium and a few yellowish-green sporangia. No visible growth of Cultures 6 and 7 was observed. The unsalted butter appeared to furnish ample food for the growth of the majority of the cultures studied.

B. Moisture

The influence of moisture on the growth of molds may be considered from two standpoints, namely, the moisture in the substrate itself and that carried by the atmosphere.

1. Moisture in Substrate

It has been shown in experiments reported in the previous pages that the presence of water facilitates the growth of molds on butterfat. As butter contains a considerable percentage of water, especially in intimate association with the most useful foodstuffs contained in the butter in the form of droplets of buttermilk, it was considered unessential to investigate the influence of water of constitution upon the growth of molds, further than that reported in previous or subsequent pages in connection with other factors.

2. Moisture in Atmosphere

a. Effect of Humidity on Growth of Molds on Unsalted Butter

Methods. Sweet cream, testing 35 per cent fat, was autoclaved, cooled, and churned in a sterile Dazey churn. The butter was washed with sterile water and worked with sterile paddles, due precautions being taken to prevent contamination. Small blocks of the finished butter were placed in sterile petri plates and held over night at 0° C. in order to harden the butter. The following day the cultures were streaked over the surfaces of the samples. The plates were kept at 10° to 12° C. for 6 weeks, one set in the metal humidor at a relative humidity of 100 per cent, and the other set in the laboratory at a relative humidity of 70 to 75 per cent.

Results. The comparison between the growth of the molds on the samples of butter kept at different humidities is shown in Table XXXII. At the end of 6 weeks, none of the butters kept at the lower humidity gave any evidence of growth. In the samples kept in an atmosphere saturated with moisture, Cultures 1 and 4 produced dark green smudgy areas that spread some distance from the line of inoculation; Culture 5 showed delicate, white, aerial threads of mycelium, bearing smoky-gray and black sporangia; Culture 6 produced a slight, white feltlike mass; Cultures 8 and 9 formed white and green spots scattered over the surface and also gave to the butter a distinctly Roquefort cheese

TABLE XXXII

Effect of Humidity upon Growth of Mold Cultures Inoculated on Surface of Sterile, Unsalted Butter

Culture	Extent of growth at 10 12° C., after									
	1 week		2 weeks		3 weeks		4 weeks		6 weeks	
	Dry	Humid	Dry	Humid	Dry	Humid	Dry	Humid	Dry	Humid
1. *A't. humicola*	—	—	—	—	—	+G	—	+++	—	++++
2. *A. flavus*	—	—	—	—	—	—	—	—	—	—
3. *A. niger*	—	—	—	—	—	—	—	—	—	—
4. *H. cladosporioides* ..	—	—	—	—	—	+G	—	+++	—	+++
5. *M. sylvaticus*	—	—	—	—	—	—	—	+WB	—	+
6. *O. lactis var. A.* ...	—	—	—	—	—	—	—	+W	—	+
7. *O. lactis var. B.* ...	—	—	—	—	—	—	—	—	—	—
8. *P. biforme*	—	+W	—	+	—	++	—	++	—	++++WG
9. *P. expansum*	—	+W	—	+	—	++	—	++WG	—	+++
10. *R. nigricans*	—	—	—	—	—	—	—	+W	—	+
Check	—	—	—	—	—	—	—	—	—	—

TABLE XXXIII

Effect of Humidity upon Growth of Mold Cultures on Unsalted Butter Churned from Inoculated Sterile Cream

Culture	Extent of growth at 20–25° C., after									
	1 week		2 weeks		3 weeks		4 weeks		6 weeks	
	Dry	Humid	Dry	Humid	Dry	Humid	Dry	Humid	Dry	Humid
1. *Alt. humicola*	—	—	—	—	—	—	—	—	—	—
2. *A. flavus*	—	+WY	+W	+	+	++YG	+	++	+	++
3. *A. niger*	—	+B	—	+	—	+	—	+	—	+
4. *H. cladosporioides* ..	++G	++G	+++	+++	+++	+++	+++	+++	+++	+++
5. *M. sylvaticus*	—	+W	—	++	—	++	—	++	—	++
6. *O. lactis var. A.* ...	—	—	—	—	—	—	—	—	—	—
7. *O. lactis var. B.* ...	—	—	—	—	—	—	—	—	—	—
8. *P. biforme*	—	+W	+W	+	+	+	+	+	+	+
9. *P. expansum*	—	+G	—	++	—	++	—	++	—	++
10. *R. nigricans*	—	—	—	—	—	—	—	—	—	—
Check	—	—	—	—			—	—	—	—

odor; Culture 10 developed a scanty, white aerial mycelium. There were no signs of growth with Cultures 2 and 3. It will be pointed out later that these cultures do not grow well at 10° C. and for this reason did not develop on the samples studied in this trial.

b. Effect of Humidity on the Growth of Molds on Unsalted Butter Churned from Inoculated Cream

Methods. Eleven lots of sweet, 40 per cent cream were placed in Erlenmeyer flasks and autoclaved. When they were cool, they were inoculated with the cultures being studied, except one lot which was held as a check. The inoculated creams were allowed to stand at room temperature (20° to 25° C.) for 4 days after which they were placed at 0° C. until cooled sufficiently to churn. During the 4 days, all the cultures had grown extremely well and covered the surface of the cream with a deep layer of mycelium bearing the characteristic fruiting bodies. Each lot of cream was churned in a sterile Dazey churn, the butter washed with sterile water and worked with sterile paddles under careful conditions. Pieces of the feltlike mass formed by the mycelium were removed as far as possible from the butter. Small blocks of the butter were placed in petri plates. One cc. of water was placed in each of the plates of one set of samples and replenished daily, while the other set was left without water. Both lots were incubated at 20° to 25° C. for 6 weeks.

Results. Table XXXIII shows that some of the samples maintained at low humidities showed the growth of mold after one or 2 weeks but in most cases the development on the samples at higher humidities gave evidence of more favorable growing conditions. Culture 4 became clearly visible after one week under both conditions, and produced a very dark green smudge and surface spots. A delicate white web of mycelium was formed by Culture 2 on the dry samples, but bright yellowish-green sporangia on the butter well supplied with moisture. Culture 8 produced white spots under both conditions. There were no visible signs of growth in Cultures 1, 6, 7, and 10.

C. Temperature

That temperature has a profound effect upon the growth of microörganisms is generally appreciated. Each species has its minimum, optimum, and maximum temperatures, which vary with the conditions under which the organisms are existing. Butter is kept at a wide range of storage temperatures but these are, in most cases, near 0° C. or below. Occasionally, lots of butter will be exposed to higher temperatures for considerable periods of time. The ten species of molds used in these experiments were seeded on various substrata in order to observe the effect of different temperatures upon their growth. The temperatures used did not go below 0° C. but subsequent studies should be pursued at lower temperatures for extended periods.

1. Growth on Whey Broth

Methods. Fresh skimmilk was heated to 35° C. and maintained at that temperature while dilute hydrochloric acid was added slowly, with constant stirring. The milk was brought to the isoelectric point of casein, pH 4.6 to 4.7 by comparison with methyl red standards. The finely granulated casein was removed by filtering through cheesecloth. The resultant whey was autoclaved for 15 minutes to coagulate the heat-labile proteins and filtered through cotton. The whey was neutralized with N/1 sodium hydroxide to pH 6.8, and 0.5 per cent Bacto peptone was added. The mixture was autoclaved for 15 minutes to precipitate the acid-soluble substances and filtered through paper, after which it was tubed and sterilized. Three sets of inoculated samples were prepared. One set was stored at 20° to 25° C. and 40 to 50 per cent relative humidity, another set at 10° to 12° C. and 70 to 75 per cent humidity, and the other at 0° to 2° C. and 70 to 75 per cent humidity.

Results. Table XXXIV gives the results of this experiment. It is evident that all the cultures found the whey broth an excellent source of food, as shown by the active growth at 20° C. after one week. A certain amount of subsurface mycelium was present in most cases, especially after 3 weeks at this temperature. Culture 2 was very slow to develop at 10° C. and when it did the mycelium was scanty. Culture 3 likewise made slight progress at this temperature. The growth of all cultures was retarded when the whey broth was kept at 0° C. Cultures 2, 3, and 10 gave no evidence of growth within 3 weeks. Cultures 1 and 5 produced traces of visible mycelium in the depths of the liquids. Time was an apparent factor at the lower temperatures, altho certain of the species showed no growth after longer periods of incubation.

2. Growth on Whey Agar Slants

Methods. A solid medium containing 1.2 per cent Bacto agar was prepared from whey broth made according to the method outlined in the previous experiment. This medium was tubed, autoclaved, and slanted. After inoculation, the three sets of samples were stored under the conditions described in the foregoing trial.

Results. All the cultures grew luxuriantly after one week at 20° C., as indicated in Table XXXV. Except Culture 2, which failed to grow, and Culture 3 which developed poorly, all showed practically normal growth at 10° C. At 0° C. the development of cultures that grew at all was less luxuriant. Cultures 2, 3, and 10 failed to produce

TABLE XXXIV

Effect of Temperature upon Growth of Mold Cultures in Whey Broth

Culture	Extent of growth at ordinary humidity, after								
	1 week			2 weeks			3 weeks		
	20° C.	10° C.	0° C.	20° C.	10° C.	0° C.	20° C.	10° C.	0° C.
1. *Alt. humicola*	++++(++)	+(++)	—(+)	++++(+)	+(++)	—(+)	++++(++)	++(++)	—(+)
2. *A. flavus*	++++(++)	—	—	++++(++)	—	—	++++(++)	+	—
3. *A. niger*	++++	+	—	++++	+(+)	—	++++(++)	+(+)	—
4. *H. cladosporioides* .	++++	+++(+)	+	++++	+++(+)	++(+)	++++	+++(+)	++(+)
5. *M. sylvaticus*	+++(++)	++(++)	—	+++(++)	++(++)	—(+)	+++(++)	++(++)	—(++)
6. *O. lactis var. A.* ..	++++	+++(+)	+(+)	++++	+++(+)	+(+)	++++	+++(+)	+(+)
7. *O. lactis var. B.* ..	+++(++)	+++(++)	—(+)	++++(++)	+++(++)	—(+)	++++(+)	++(+)	+(+)
8. *P. biforme*	++++(+)	+++(+)	+	++++(+)	+++(+)	+(+)	++++(+)	++++(+)	+(+)
9. *P. expansum*	+++(+)	+++(+)	—	++++(+)	+++(+)	—(+)	++++(+)	+++(+)	+(+)
10. *R. nigricans*	++++(++)	++(++)	—	++++(++)	+++(+)	—	++++(++)	+++(+)	—
Check	—	—	—	—	—	—	—	—	—

TABLE XXXV

Effect of Temperature upon Growth of Mold Cultures on Whey Agar

Culture	Extent of growth at ordinary humidity, after								
	1 week			2 weeks			3 weeks		
	20° C.	10° C.	0° C.	20° C.	10° C.	0° C.	20° C.	10° C.	0° C.
1. *Alt. humicola*	++++	+++	+	++++	++++	+	++++	++++	++
2. *A. flavus*	++++	—	—	++++	—	—	++++	—	—
3. *A. niger*	+++	+	—	+++	+	—	+++	+	—
4. *H. cladosporioides*	++++	++++	+	++++	++++	++	++++	++++	++
5. *M. sylvaticus*	+++	++	+	++++	++	+	++++	++	++
6. *O. lactis var. A.*	+++	+++	+	++++	+++	+	++++	+++	++
7. *O. lactis var. B.*	+++	+++	+	++++	+++	+	++++	+++	+
8. *P. biforme*	++++	++++	++	++++	++++	++	++++	++++	+++
9. *P. expansum*	++++	+++	+	++++	+++	+	++++	+++	+
10. *R. nigricans*	++++	++++	—	++++	++++	—	++++	++++	—
Check	—	—	—	—	—	—	—	—	—

visible mycelium. Low temperatures had a marked effect on the growth, especially with Cultures 2 and 3.

3. Growth in Sweet Buttermilk

Methods. Buttermilk was obtained from a churning of fresh, sweet cream, tubed, and autoclaved. The inoculated samples were divided into three lots and incubated under the conditions explained in the last two experiments.

Results. Table XXXVI shows that the cultures kept at 20° C. did not develop as promptly in the buttermilk as they did in whey broth or whey agar. Growth at the end of 3 weeks was reasonably good in all cases. The development at 10° C. was somewhat less in most instances. Culture 2 showed no visible growth, Culture 3 gave barely visible growth after 3 weeks. Cultures 2, 3, and 10 again failed to grow at 0° C. during the observation period. In general, the surface growth on buttermilk was somewhat less than it had been on whey broth and whey agar.

4. Growth on Sterile Butter

Methods. A batch of sweet cream was autoclaved and, after cooling, churned in a sterile Dazey churn. The butter was washed with sterile water and worked with sterile paddles. The finished butter was divided into four portions, one of which was left unsalted. Sterile salt was worked into the other lots of butter in varying amounts, giving a final salt content (by analysis) of 1.2 per cent, 2.6 per cent, and 2.9 per cent, respectively. Blocks of each lot of butter were placed in petri plates and allowed to harden over night at 0° C. The samples were inoculated by streaking the cultures across the surface. One set of samples was incubated at 0° C. and the other at 10° C. in the metal humidors, at a relative humidity of 100 per cent.

Results. The observations made on the samples over a period of 6 weeks are reported in Table XXXVII. At 0° C., Culture 9 showed growth after 2 weeks, Culture 1 after 4 weeks, and Culture 8 after 6 weeks in the unsalted butter; none of the others showed any apparent development even after 6 weeks. Cultures 1 and 8 produced small white spots at this temperature in the butter containing 1.2 per cent salt. Otherwise, growth of all cultures was retarded by the combined influence of low temperature and salt. At 10° C. growth in the unsalted butter was extensive in most instances and after 6 weeks, Cultures 1 and 4 produced dark green smudges, Cultures 5 and 10 developed slight aerial mycelia, Culture 6 showed a small amount of white mycelium, and Cultures 8 and 9 formed white and green spots. Cultures 2 and 3 were not able to grow. In the butter containing 1.2 per cent of salt, and kept at 10° C., Culture 5 produced a few aerial

TABLE XXXVI

Effect of Temperature upon Growth of Mold Cultures in Sweet Buttermilk

Culture	Extent of growth at ordinary humidity, after								
	1 week			2 weeks			3 weeks		
	20° C.	10° C.	0° C.	20° C.	10° C.	0° C.	20° C.	10° C.	0° C.
1. *Alt. humicola*	+	++	—	++	++	—	+++	+++	+
2. *A. flavus*	+++	—	—	+++	—	—	++++	—	—
3. *A. niger*	++	—	—	+++	—	—	++++	+	—
4. *H. cladosporioides*	++++	++	—	++++	++	—	++++	+++	++
5. *M. sylvaticus*	+++	+++	++	+++	+++	++	++++	+++	++
6. *O. lactis var. A.*	++++	++	++	++++	++	++	++++	++	++
7. *O. lactis var. B.*	++++	++	++	++++	++	++	++++	++	++
8. *P. biforme*	+++	+++	+++	+++	+++	+++	+++	+++	+++
9. *P. expansum*	+++	++	++	+++	++	++	+++	+++	++
10. *R. nigricans*	++++	+	—	++++	++	—	++++	++	—
Check	—	—	—	—	—	—	—	—	—

TABLE XXXVII

Effect of Temperature upon Growth of Mold Cultures on Sterile Butter

Culture	Extent of growth, at high humidities, after 6 weeks							
	Unsalted		1.2 per cent salt		2.6 per cent salt		2.9 per cent salt	
	10° C.	0° C.	10° C.	0° C.	10° C.	0° C.	10° C.	0° C.
1. *Alt. humicola*	++++G	+W	++G	+W	+G	—	+WG	—
2. *A. flavus*	—	—	—	—	—	—	—	—
3. *A. niger*	—	—	—	—	—	—	—	—
4. *H. cladosporioides*	+++G	—	++G	—	+G	—	+G	—
5. *M. sylvaticus*	+W	—	+W	—	—	—	—	—
6. *O. lactis var. A.*	+W	—	—	—	—	—	—	—
7. *O. lactis var. B.*	—	—	—	—	—	—	—	—
8. *P. biforme*	++++WG	+W	++WG	+G	++G	—	++WG	—
9. *P. expansum*	+++WG	+G	++G	—	++G	—	++G	—
10. *R. nigricans*	+W	—	—	—	—	—	—	—
Check	—	—	—	—	—	—	—	—

Note: The same series of samples, maintained at the same temperatures, but at low humidity, failed to show any evidence of growth during 6 weeks.

hyphae; Cultures 1, 4, 8, and 9 grew quite well and produced distinct areas of moldiness. The butters containing 2.6 per cent and 2.9 per cent salt showed slight growth of Cultures 1, 4, 8, and 9. The low temperatures clearly restrained the growth of most of the species studied, and the effect became more noticeable as the percentage of salt increased.

5. Growth on Butter Made from Inoculated Cream

Methods. Eleven batches of fresh sweet cream in flasks were autoclaved and cooled, after which ten lots were inoculated with the experimental cultures and the other left as a check. The inoculated cream samples were kept at 20° to 25° C. for 4 days. During this time, all cultures grew exceedingly well and produced a surface felt with normal fructification. These samples were churned in individual, sterile Dazey churns. The butter was washed with sterile water and worked with sterile paddles. Visible pieces of the felt were removed, as far as possible. Each lot of butter was divided into four parts—one remained unsalted, the others were worked with different amounts of sterile salt in order to obtain varying concentrations. The actual salt content in the different lots of butter varied as indicated in Table XXXVIII. It was very difficult to obtain exactly the same results in each case, because of the difficulty of working the butter under aseptic conditions. Blocks of the butters were placed in petri plates and hardened at 0° C. One set of plates was placed at 20° to 25° C., another at 10° to 12° C., and another at 0° to 2° C. in the metal humidors at a relative humidity of 100 per cent and observations were made during 6 weeks.

Results. The combined effect of temperature and salt concentration on the growth of the various species is shown in Table XXXVIII. It will be noted that Cultures 1, 6, 7, and 10 failed to make any visible growth under any conditions. Cultures 2 and 3 grew reasonably well at 20° C. in all salt concentrations but apparently could not develop at 10° or 0° C. Culture 4 grew at all three temperatures but was affected by increased percentages of salt, especially at 0° C. The only visible growth secured with Culture 5 was on the unsalted sample at 20° C. Results with Culture 8 were irregular, but it grew at all temperatures. With the higher salt concentrations and lower temperatures its development was retarded or checked. Culture 9 was not affected particularly by the salt content of the butter but failed to appear at 0° C. Evidently, the effect of temperature varied with the species of mold and the composition of the substrate as influenced by the salt content.

D. Atmosphere

Most species of molds are considered aerobic, or at least facultative, and this indicates that a satisfactory supply of oxygen is a factor

TABLE XXXVIII

Effect of Temperature upon Growth of Mold Cultures in Butter from Inoculated Cream

Culture	Per cent of salt	Extent of growth, high humidity, after								
		2 weeks			4 weeks			6 weeks		
		20° C.	10° C.	0° C.	20° C.	10° C.	0° C.	20° C.	10° C.	0° C.
1. *Alt. humicola*	0	—	—	—	—	—	—	—	—	—
	1.5	—	—	—	—	—	—	—	—	—
	2.7	—	—	—	—	—	—	—	—	—
	4.2	—	—	—	—	—	—	—	—	—
2. *A. flavus*	0	+	—	—	++	—	—	++	—	—
	1.4	++	—	—	+++	—	—	+++		—
	2.2	+++	—	—	+++	—	—	+++	—	—
	4.0	++	—	—	++	—	—	++	—	—
3. *A. niger*	0	+	—	—	+	—	—	+		—
	1.5	++	—	—	+++	—	—	+++	—	—
	2.5	++	—	—	++	—	—	++	—	—
	4.5	++	—	—	++	—	—	++	—	—
4. *H. cladosporioides* ..	0	+++	++	+	+++	+++	++	+++	++++	++
	1.6	++	++	—	++	+	+	++	+	+
	2.7	++	+	—	+	+	—	+	+	—
	3.3	+	++	—	+	+	—	+	+	—
5. *M. sylvaticus*	0	++	—	—	++	—	—	++	—	—
	1.1	—	—	—	—	—	—	—	—	—
	2.3	—	—	—	—	—	—	—	—	—
	3.5	—	—	—	—	—	—	—	—	—
6. *O. lactis var. A.* ...	0	—	—	—	—	—	—	—	—	—
	1.4	—	—	—	—	—	—	—	—	—
	1.6	—	—	—	—	—	—	—	—	
	3.0	—	—	—	—	—	—	—	—	—
7. *O. lactis var. B.* ...	0	—	—	—	—	—	—	—	—	—
	0.9	—	—	—	—	—	—	—	—	—
	2.1	—	—	—	—	—	—	—	—	—
	3.1	—	—	—	—	—	—	—	—	—
8. *P. biforme*	0	+	+	+	+	++	++	+	++	++
	0.7	—	+	—	—	++	—	—	++	+
	2.3	+	—	—	+	++	—	+	++	—
	3.1	+	—	—	+	—	—	+	—	—
9. *P. expansum*	0	++	+	—	++	++	—	++	++	—
	1.3	++	+	—	++	++	—	++	++	—
	2.2	++	+	—	++	++	—	++	++	—
	3.0	+	+	—	+	++	—	+	++	—
10. *R. nigricans*	0	—	—	—	—	—	—	—	—	—
	1.3	—	—	—	—	—	—	—	—	—
	2.1	—	—	—	—	—	—	—	—	—
	4.0	—	—	—	—	—	—	—	—	—
Check	0.0	—	—	—	—	—	—	—	—	—

in their growth. Experiments were undertaken to determine how the mold growth on butter might be affected by changes in atmospheric conditions.

1. Ordinary Air Supply

In the experiments previously reported, and in which a plentiful supply of oxygen was provided, the species of molds making up the experimental group were able to grow satisfactorily when the food supply, moisture, temperature, and other conditions were favorable. These results may be considered as checks demonstrating that the molds grew well when an abundant supply of air was present.

2. Reduced Air Supply—Partial Vacuum

Methods. Sterile cream was churned in a sterile Dazey churn. The butter was washed with sterile water and worked with sterile paddles. Blocks of butter were placed in petri plates (in which the covers were kept slightly raised by the use of small wire staples) and hardened at 0° C. The surface of the butter was inoculated with the molds being studied. The plates were then placed in an ordinary sterile glass desiccator. After a liter of water was placed in the the bottom of the jar to provide adequate humidity, the lid was put in place and sealed with vaseline. A vacuum of 25 inches was drawn and maintained during the period of study. The temperature of incubation was 20° to 25° C.

Results. The results of the trial are given in Table XXXIX. Growth was not very active during the first week but increased somewhat during the subsequent 3 weeks. The development was never very great, however, and was not comparable with that obtained under ordinary atmospheric conditions. The reduction of the amount of available oxygen appeared to retard the development of these species.

TABLE XXXIX

EFFECT OF REDUCED AIR SUPPLY UPON GROWTH OF MOLD CULTURES ON STERILE, UNSALTED BUTTER

Extent of growth, at 20 25° C., high humidity, under 25 inches of vacum, after	Culture No.*										
	1	2	3	4	5	6	7	8	9	10	Check
1 week	+	+	+	+	−	−	−	+	−	−	−
4 weeks	+	++	++	++	+	−	+	++	+++	+	−

* See Table XXXVIII for species.

3. Partial Removal of Carbon Dioxide

Methods. The butter used was prepared in the same manner as that for 2, above. The plates were held in a sterile desiccator in the bottom of which was placed a liter of a 10 per cent aqueous solution of sodium hydroxide. This was added to absorb some of the carbon dioxide; at the same time it was a source of moisture. The lid of the desiccator was sealed with vaseline. The temperature of incubation was 20° to 25° C.

TABLE XL

EFFECT OF PARTIAL REMOVAL OF CARBON DIOXIDE FROM ATMOSPHERE UPON GROWTH MOLD CULTURES ON STERILE, UNSALTED BUTTER

Extent of growth at 20–25° C., high humidity, (10% soln. of NaOH) in desiccator, after	Culture No.*										
	1	2	3	4	5	6	7	8	9	10	Check
1 week	+	+	+	+	+	+	+	++	++	++	–
4 weeks	+++	++	+++	+++	++++	+	+	+++	+++	++++	–

* See Table XXXVIII for species.

Results. Altho the growth of the cultures was not extensive during the first week, Table XL shows that excellent development of all except Cultures 6 and 7 occurred after 4 weeks. However, the last-named cultures actually showed more visible growth under these conditions than they had shown at any other time when seeded on butter. Apparently, a reduction in the amount of carbon dioxide does not seriously deter the growth of the species under observation.

4. Removal of Oxygen

Methods. The butter used was prepared in the manner described in 2 and 3, above. The plates were placed in a sterile desiccator and the lid sealed with vaseline, after 100 grams of pyrogallic acid had been placed in the bottom. A funnel was introduced through an opening in the side of the desiccator and 500 cc. of a 10 per cent aqueous solution of sodium hydroxide were added to the pyrogallic acid. The funnel was removed quickly and the opening closed and sealed. The temperature of incubation was 20° to 25° C.

TABLE XLI

EFFECT OF REMOVAL OF OXYGEN FROM THE ATMOSPHERE UPON THE GROWTH OF MOLD CULTURES ON STERILE, UNSALTED BUTTER

(Oxygen exhausted by NaOH–pyrogallic acid mixture)

Extent of growth at 20–25° C., high humidity, after	Culture No.*										
	1	2	3	4	5	6	7	8	9	10	Check
1 week	–	–	–	–	–	–		–	–	–	–
4 weeks	–	–	–	–	–	–	–	–	–	–	–

* See Table XXXVIII for species.

Results. Table XLI points out clearly that no growth appeared in any of the samples even after 4 weeks. The exhaustion of oxygen apparently made conditions unfavorable for the development of the molds being studied.

E. Miscellaneous Chemical and Physical Factors

1. Salt Content

Sodium chloride has been considered a food preservative for many years. As most butter contains some salt, and as unsalted butter has appeared to be more susceptible to molding than the salted type, experiments were conducted to determine the effect of various concentrations of sodium chloride upon the growth of the species of molds selected for this study.

a. Whey Broth Plus Salt

Methods. Whey broth prepared in the manner described in previous experiments was used as a substrate. Sodium chloride was added to various portions in different amounts, so the final salt content (by weight) in the different lots of broth was 10, 15, and 20 per cent. An unsalted portion was left as a check. The solutions were tubed and autoclaved. After inoculation the samples were placed at 20° to 25° C. in a room with a relative humidity of 40 to 50 per cent, and observed for 3 weeks.

Results. The record of the observations is given in Table XLII. The growth of all the cultures was excellent in the unsalted broth, especially on the surface. In the broth containing 10 per cent of salt, Cultures 2, 3, 4, 8, and 9 had produced abundant mycelium and fructification at the end of 3 weeks. Cultures 1, 5, and 10 produced only subsurface growth; Cultures 6 and 7 were checked entirely. In the 15 per cent salt broth, Cultures 2, 8, and 9 grew fairly well on the surface; Cultures 1, 3, and 4 showed some subsurface mycelium. The remaining cultures gave no growth with 20 per cent salt. The only species to show any development in this broth were Cultures 8 and 9 and they grew well. It is evident that salt exercised a restraining effect upon the growth of molds but it varied considerably with the different species.

b. Whey Agar Plus Salt

Methods. The whey agar used in this experiment was similar to that described previously. Sodium chloride was added to portions of the medium so that the final concentrations by weight were 10, 15, and 20 per cent. These and the unsalted check were tubed, autoclaved, and slanted. After inoculation they were incubated under conditions similar to those in the preceding experiment.

Results. All cultures developed luxuriantly on the unsalted slants, as reported in Table XLIII. In the 10 per cent salt agar, Cultures 6 and 7 were the only ones that failed to grow, altho Cultures 5 and 10 showed very meager growth. When the salt content reached 15 per cent, Cultures 2, 8, and 9 showed moderate growth and Cultures

TABLE XLII

Effect of Salt upon Growth of Mold Cultures on Whey Broth

Culture	Extent of growth at 20–25° C., ordinary humidity, after											
	1 week				2 weeks				3 weeks			
	Per cent of salt				Per cent of salt				Per cent of salt			
	0	10	15	20	0	10	15	20	0	10	15	20
1. *Alt. humicola*	++++(++)	—(+)	—	—	++++(++)	—(++)	—	—	++++(++)	—(++)	—(+)	—
2. *A. flavus*	++++(++)	+++	++	—	++++(++)	+++(+)	++(+)	—	++++	+++(+)	++(+)	—
3. *A. niger*	++++	+++(+)	—	—	++++	+++(+)	—(++)	—	++++(++)	+++(+)	—(++)	—
4. *H. cladosporioides*	++++	+++(+)	—	—	++++	+++(+)	—	—	++++	+++(+)	—(+)	—
5. *M. sylvaticus*	+++(++)	—(+)	—	—	+++(++)	—(+)	—	—	+++(++)	—(+)	—	—
6. *O. lactis var. A.*	++++	—	—	—	++++	—	—	—	++++	—	—	—
7. *O. lactis var. B.*	+++(++)	—	—	—	++++(++)	—	—	—	++++(++)	—	—	—
8. *P. biforme*	++++(+)	+++(+)	++	—	++++(+)	+++(+)	+++(+)	+	++++(++)	+++(+)	++(+)	++
9. *P. expansum*	+++(+)	+++(+)	++	+	++++(+)	+++(+)	++(+)	++	++++(+)	+++(+)	++(+)	++
10. *R nigricans*	++++(++)	—	—	—	++++(++)	—(+)	—	—	++++(++)	—	—	—
Check	—	—	—	—	—	—	—	—	—	—	—	—

TABLE XLIII

Effect of Salt upon Growth of Mold Cultures on Whey Agar

Culture	Extent of growth at 20–25° C., ordinary humidity, after											
	1 week				2 weeks				3 weeks			
	Per cent of salt				Per cent of salt				Per cent of salt			
	0	10	15	20	0	10	15	20	0	10	15	20
1. *Alt. humicola*	++++	++	—	—	++++	+++	+	—	++++	+++	+	—
2. *A. flavus*	++++	+++	++	—	++++	+++	++	—	++++	+++	++	—
3. *A. niger*	+++	+++	+	—	+++	++	+	—	+++	++	+	—
4. *H. cladosporioides*	++++	+++	—	—	++++	+++	+	—	++++	+++	++	—
5. *M. sylvaticus*	+++	+	—	—	+++	+	—	—	+++	+	—	—
6. *O. lactis var. A.*	+++	—	—	—	+++	—	—	—	+++	—	—	—
7. *O. lactis var. B.*	+++	—	—	—	+++	—	—	—	+++	—	—	—
8. *P. biforme*	++++	++++	++	+	++++	+++	++	+	++++	+++	++	+
9. *P. expansum*	++++	++	++	+	++++	++	++	+	++++	++	++	+
10. *R. nigricans*	++++	+	—	—	++++	+	—	—	++++	+	—	—
Check	—	—	—	—	—	—	—	—	—	—	—	—

1 and 4 slight growth. The others remained dormant. As in the previous experiment Cultures 8 and 9 were the only ones to grow in the 20 per cent concentration of salt and their growth was scanty. Growth was better on the solid medium than on the whey broth, but the influence of the salt was demonstrated to be in the same general direction.

c. Sterile, Sweet Buttermilk Plus Salt

Methods. Buttermilk was obtained directly from a churning of sweet cream. The necessary salt was added to yield solutions containing 5, 10, 15, and 20 per cent. An unsalted portion was kept as a check. All lots were tubed and autoclaved. After inoculation they were incubated under the conditions described under "a" and "b," above.

Results. The growth of every culture was luxuriant in the unsalted buttermilk after two weeks, as is shown in Table XLIV. In the 5 per cent buttermilk, development was excellent after 2 weeks in the case of Cultures 1, 2, 3, 4, 8, and 9, moderately good with Cultures 5 and 10, but only slight with Cultures 6 and 7. The 10 per cent salt concentration completely inhibited Cultures 5, 6, 7, and 10, but the rest grew well. When the percentage of salt was increased to 15 per cent, only Cultures 2, 3, 8, and 9 were active. With 20 per cent salt, only Culture 9 produced visible growth. It will be noted that the growth of certain species is retarded more in the salted buttermilk than in whey broth or agar.

d. Sterile, Sour Buttermilk Plus Salt

Methods. A sample of buttermilk was obtained from a churning of sour cream butter. Salt was added to portions of this buttermilk to give concentrations of 5, 10, 15, 20, and 25 per cent, and an unsalted check was retained. These solutions were tubed and autoclaved. After inoculation, they were incubated at 20° to 25° C. for 2 weeks at a relative humidity of 60 to 65 per cent.

Results. Table XLV presents the results obtained in this experiment. In the unsalted buttermilk the growth after 2 weeks was luxuriant but it had been slower than that obtained on the sweet buttermilk. The development of the cultures in the 5 per cent salt solution was practically the same as in the unsalted samples, in some cases less and in other cases greater. In the buttermilk containing 10 per cent of salt, Cultures 2, 3, 4, 8, and 9 grew well. When the concentration of salt was increased to 15 per cent, Cultures 2, 3, 8, and 9 were the only ones to produce visible mycelium and fruiting bodies. The 20 per cent solution retarded all except Culture 9, and in a 25 per cent concentration of salt none were able to grow during the 2 weeks incubation period.

TABLE XLIV

Effect of Salt upon Growth of Mold Cultures in Sweet Buttermilk

Culture	Extent of growth at 20–25° C., ordinary humidity, after									
	4 days					2 weeks				
	Per cent of salt					Per cent of salt				
	0	5	10	15	20	0	5	10	15	20
1. *Alt. humicola*	+++W	+W	—	—	—	+++G	+++WG	++G	—	—
2. *A. flavus*	++WY	++WY	++Y	—	—	+++YG	+++YG	+++YG	+W	—
3. *A. niger*	++WBr	+WBr	+Br	—	—	+++Br	+++Br	++Br	+W	—
4. *H. cladosporioides* ..	+++G	++G	+G	—	—	+++G	+++G	++G	—	—
5. *M. sylvaticus*	++W	+W	—	—	—	+++WB	++WB	—	—	—
6. *O. lactis var. A.* ...	++W	—	—	—	—	+++W	+W	—	—	—
7. *O. lactis var. B.* ...	+++W	—	—	—	—	+++W	+W	—	—	—
8. *P. biforme*	++W	+W	+W	—	—	+++G	+++G	++W	+W	—
9. *P. expansum*	+++G	++G	+WG	+WG	—	+++G	+++G	+++G	++WG	+WG
10. *R. nigricans*	+++WB	+W	—	—	—	+++WB	++WB	—	—	—
Check	—	—	—	—	—	—	—	—	—	—

TABLE XLV

Effect of Salt upon Growth of Mold Cultures in Sour Buttermilk

Culture	Extent of growth at 20 25° C., ordinary humidity, after											
	3 days						2 weeks					
	Per cent of salt						Per cent of salt					
	0	5	10	15	20	25	0	5	10	15	20	25
1. *Alt. humicola*	++W	+W	+W	—	—	—	+++WG	++G	+W	—	—	—
2. *A. flavus*	++YG	+Y	+Y	—	—	—	+++YG	+++YG	+++YG	+YG	—	—
3. *A. niger*	+WB	+B	+B	—	—	—	++B	+++B	+++B	+Br	—	—
4. *H. cladosporioides* .	+G	+G	—	—	—	—	+++G	+++G	++G	—		—
5. *M. sylvaticus*	++W	+W	—	—	—	—	+++WB	++WB	—	—	—	—
6. *O. lactis var. A.* ...	++W	+W	—	—	—	—	+++WY	++WY	—	—	—	
7. *O. lactis var. B.*	++W	+W	—	—	—	—	+++WY	++WY	—	—	—	—
8. *P. biforme*	+W	+W	+W	+W	—	—	+++G	++G	+++WY	+G	—	—
9. *P. expansum*	++WG	+WG	+W	—	—	—	+++G	+++G	+++G	++G	+W	—
10. *R. nigricans*	++W	+W	—	—	—	—	+++WB	++WB	—	—	—	—
Check			—	—	—	—	—	—	—	—	—	—

In order to determine whether the cultures that had failed to grow on the buttermilk containing 15 per cent of salt were simply retarded or actually killed, a portion of each sample was plated on whey agar. Normal colonies were obtained from all such platings, proving that the spores were still viable but unable to grow in the strong brine. In a similar way, when samples were taken from the 25 per cent solution, it was found that Cultures 2, 3, 5, 8, 9, and 10 had been unharmed by the salt while Cultures 1, 4, 6, and 7 apparently had been destroyed, as no colonies were obtained. Accordingly, it appears that moderately strong brines retard the growth of certain species; higher concentrations may actually destroy some species.

e. Sterile Butter Plus Salt

Methods. A batch of sweet cream was autoclaved, cooled, churned in a sterile Dazey churn, and the butter washed with sterile water. The butter was divided into five lots, one of which was retained without salt as a check. Sterilized salt was added in varying amounts to the other four lots. All were worked as thoroly and carefully as possible with sterile paddles. The salt contents of the four lots of salted butter, as determined by analysis, were 0.5, 0.8, 1.4, and 1.7 per cent, respectively. Small blocks of each were placed in petri plates and hardened at 0° C. over night. The next day they were inoculated by streaking the cultures across the surface. The intention was to incubate these samples at 5° to 6° C. at a high humidity for 6 weeks, but circumstances made it necessary to remove the plates from the humidor after one week. During the next 2 weeks they were kept at 5° to 6° C. but at a lower humidity. At the end of 3 weeks it was necessary to remove the samples from the cooler. For the following 3 weeks they were kept at 20° to 25° C. at a high humidity. Consequently, conditions were so variable that results are not very satisfactory. Analyses of the butters showed the following compositions:

	Per cent				
Salt	0.0	0.5	0.8	1.4	1.7
Water	14.0	14.4	14.2	14.2	14.8
Salt in brine	0.0	3.4	5.3	8.9	10.3

This makes it possible to interpret the results in terms of those obtained with buttermilk, whey broth etc.

Results. The results of this trial are recorded in Table XLVI. No growth was visible in any of the samples held at 6° C. during the 2 weeks, except Culture 9, which had produced a small white spot in the unsalted butter. After 3 weeks, Cultures 1, 4, and 9 had developed visible colored areas in the unsalted butter. The following week witnessed the growth of Cultures 3 and 10 in addition to those mentioned. After

TABLE XLVI

EFFECT OF SALT UPON GROWTH OF MOLD CULTURES ON STERILE BUTTER

Culture	Extent of growth, 1st week at 6° C., high humidity; 2nd and 3rd weeks at 6° C., ordinary humidity; 4th, 5th, and 6th weeks at 20-25° C., high humidity, after														
	1 week					3 weeks					6 weeks				
	Per cent of salt					Per cent of salt					Per cent of salt				
	0	0.5	0.8	1.4	1.7	0	0.5	0.8	1.4	1.7	0	0.5	0.8	1.4	1.7
1. *Alt. humicola*	—	—	—	—	—	+WG	—	—	—	—	+++G	++G	++G	++G	+G
2. *A. flavus*	—	—	—	—	—	—	—	—	—	—	+W	++Y	+Y	+Y	+++YG
3. *A. niger*	—	—	—	—	—	—	—	—	—	—	+++B	+++B	++B	++B	++B
4. *H. cladosporioides* ..	—	—	—	—	—	+G	—	—	—	—	+++G	+++G	++G	++G	++G
5. *M. sylvaticus*	—	—	—	—	—	—	—	—	—	—	++WB	++W	—	—	—
6. *O. lactis var. A.* ...	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7. *O. lactis var. B.* ...	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8. *P. biforme*	—	—	—	—	—	—	—	—	—	—	+W	+G	+W	+W	+W
9. *P. expansum*	—	—	—	—	—	+W	—	—	—	—	+++G	+++G	+++G	+++G	+++G
10. *R. nigricans*	—	—	—	—	—	—	—	—	—	—	++W	++W	—	—	—
Check	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE LXVII

EFFECT OF SALT UPON GROWTH OF MOLD CULTURES ON STERILE BUTTER

Culture	Extent of growth at 10° C., high humidity, after											
	1 week				3 weeks				6 weeks			
	Per cent of salt				Per cent of salt				Per cent of salt			
	0	1.2	2.6	2.9	0	1.2	2.6	2.9	0	1.2	2.6	2.9
1. *Alt. humicola*	—	—	—	—	+G	—	—	—	++++G	++G	+G	+WG
2. *A. flavus*	—	—	—	—	—	—	—	—	—	—	—	—
3. *A. niger*	—	—	—	—	—	—	—	—	—	—	—	—
4. *H. cladosporioides*	—	—	—	—	+G	—	—	—	+++G	++G	+G	+G
5. *M. sylvaticus*	—	—	—	—	—	—	—	—	+W	+W	—	—
6. *O. lactis var. A.* ...	—	—	—	—	—	—	—	—	—	—	—	—
7. *O. lactis var. B.*	—	—	—	—	—	—	—	—	—	—	—	—
8. *P. biforme*	+W	—	—	—	++W	+W	—	—	++++WG	++WG	++G	++WG
9. *P. expansum*	+W	—	—	—	++W	+W	—	—	+++WG	++G	++G	++G
10. *R. nigricans*	—	—	—	—	—	—	—	—	+W	—	—	—
Check	—	—	—	—	—	—	—	—	—	—	—	—

2 weeks at room temperature active development was observed for all cultures except 6 and 7. At the end of 6 weeks, Cultures 1, 2, 3, 4, 8, and 9 had shown some growth in all samples, salted and unsalted, but greatest in the latter. Cultures 5 and 10 were checked by the salt in the butter containing 0.8 per cent or more. Cultures 6 and 7 did not grow at all. When it is realized that the highest salt concentration on the basis of brine was 10.3 per cent in the butter containing 1.7 per cent of salt, it is not surprising that some species were able to grow, as the same cultures had demonstrated their ability to do so in buttermilk containing an equivalent amount of salt. The checking of the growth of Cultures 5 and 10 in butter with a percentage of salt in brine of more than 5.3 per cent also is in accordance with the results obtained in buttermilk. These facts emphasize the importance of considering the salt content of butter in terms of the percentage of salt in brine when it is to be taken into account as a preservative or deterrent of mold growth.

f. Sterile Butter Plus Salt

Methods. Sweet cream was autoclaved, cooled, churned in a Dazey churn, and the butter washed with sterile water. The butter was divided into four lots, one of which was left unsalted to serve as a check. Sterile salt was added to the three portions in amounts sufficient to give final salt contents of 1.2, 2.6, and 2.9 per cent, respectively. Each lot of butter was worked separately with sterile paddles and under aseptic conditions. Blocks of each butter were placed in petri plates and held at 0° C. over night for hardening. The samples were inoculated on the surface and placed in the metal humidor and stored at 10° C. for 6 weeks at a relative humidity of 100 per cent.

The composition of these four lots of butter as determined by analysis was as follows:

	Per cent			
Salt	0.0	1.2	2.6	2.9
Water	15.9	15.6	16.0	16.0
Salt in brine	0.0	7.1	13.9	15.3

Results. The data are reported in Table XLVII. Cultures 8 and 9 were the only ones to show growth during the first 2 weeks and then only on the unsalted butter. After 3 weeks Cultures 1 and 4 grew on the unsalted butter; Cultures 8 and 9 also developed on the butter containing 1.2 per cent salt. Cultures 1, 4, 8, and 9 developed extensively in the unsalted butter after 4 weeks and Cultures 5, 6, and 10 became barely visible. In the butter containing 1.2 per cent salt, Cultures 1, 4, 8, and 9 grew slightly. Culture 1 produced a small dark green spot on the butter with 2.6 per cent salt; Cultures 8 and 9 grew on both the 2.6 per cent and the 2.9 per cent samples. During the 6 weeks, Cultures 1, 4, 8, and 9 developed exceedingly well, but Cultures 5 and 10 set up scanty aerial mycelium, in the unsalted butter. In the butter containing 1.2 per cent salt, Cultures 1, 4, 8, and 9 grew extensively, and Culture 5 sparsely. On the butters with the higher salt concentrations, Cultures 1, 4, 8, and 9 produced fairly distinct discolorations. These results are more or less in accordance with previous observations of the growth of these molds on media containing salt, when the salt content is considered from the standpoint of its concentration in the brine. The failure of Cultures 6 and 7 to show visible growth even in unsalted butter has been the rule, altho evidence leads to the belief that they actually may be growing even tho a visible mycelium does not appear. The explanation of the failure of Cultures 2 and 3 to develop may be found in the temperature of incubation. Previous observations demonstrated that these species did not grow well in the most favorable substrate at temperatures as low as 10° C., also that a set of samples similar to those considered in Table XLVII was kept at the same temperature but at a relative humidity of 70 to 75 per cent. These samples gave no sign of growth after 3 weeks.

g. Butter Made from Inoculated Cream Plus Salt

Methods. The butter was made from sterile cream inoculated and handled according to the procedure outlined under "b" on page 47. The butter in each case was divided into four lots and worked with varying percentages of salt. The amount of salt in each lot is indicated in Table XLVIII. Considerable difficulty was encountered in churning the cream inoculated with Culture 10. It took more than an hour, while ordinarily the churning period was 10 or 15 minutes. At the other extreme, only 2 minutes were required to churn the creams containing Cultures 2 and 3. In these three samples the water content was exceedingly high and the butter little more than a paste. The percentage of water in the various samples was as follows:

Culture	Water %
1	16.8 to 19.4
2	46.2 to 50.8
3	35.0 to 36.8
4	18.4 to 20.0
5	15.0 to 19.4
6	21.0 to 21.8
7	21.6 to 23.4
8	15.0 to 19.5
9	19.2 to 20.2
10	47.4 to 51.2

The percentage of salt in brine under these conditions is as follows:

Culture	Salt in Brine %			
1	0	7.2	13.8	18.4
2	0	2.9	4.5	7.3
3	0	3.9	5.9	11.4
4	0	7.4	12.4	15.2
5	0	9.3	12.7	15.3
6	0	6.0	6.9	12.5
7	0	4.0	8.2	12.1
8	0	4.5	11.3	13.3
9	0	6.2	10.3	12.9
10	0	2.5	4.2	7.8

The butter samples were stored for 6 weeks at a temperature of 20° to 25° C. Each plate contained one cc. of added water, which was replenished at intervals to maintain a high humidity.

Results. The results of this experiment are shown in Table XLVIII. Cultures 1, 6, 7, and 10 failed to give any visible evidence of growth, altho alterations in the aroma of the butter were marked. Culture 5 showed some development of aerial mycelium in the unsalted but was not able to grow in the salted butter. The other cultures gave irregular results that are not easy to explain, but Cultures 2, 3, 4, 8, and 9 showed a tendency to grow at all salt concentrations used; the trend being toward less growth in the most highly salted sample. Plate IV illustrates the character of the growth of Culture 4 on butters containing various amounts of salt. The unsalted sample would scarcely be recognized as butter.

DISCUSSION OF RESULTS

The data obtained in the experiments reported in the preceding pages give clues to some of the important factors influencing the growth of molds in butter. For convenience, these factors will be discussed in the order in which they were studied.

Food supply.—As pointed out in the review of literature, microörganisms must have sufficient and satisfactory nutrients if they are to develop and carry on the metabolic processes of growing cells. While certain types of organisms are able to subsist on compounds that are practically pure inorganic substances, the majority of the familiar forms require a diversity of foodstuffs. It is generally agreed that fungi seek, especially, compounds containing carbon, oxygen, hydrogen, and nitrogen, particularly in the form of organic substances. In nature, most of the materials carrying these four elements also contain others, such as phosphorus, sulphur, and a great variety of mineral elements, either intimately as a part of such compounds, or as impurities. The familiar substances commonly classed as fats, proteins, carbohydrates,

TABLE XLVIII

Effect of Salt upon Growth of Mold Cultures in Butter Made from Inoculated Cream

Culture	Per cent of salt	Extent of growth at 20–25° C., high humidity, after					
		1 week	2 weeks	3 weeks	4 weeks	5 weeks	6 weeks
1. *Alt. humicola* ...	0.0	—	—	—	—	—	—
	1.5	—	—	—	—	—	—
	2.7	—	—	—	—	—	—
	4.2	—	—	—	—	—	—
2. *A. flavus*	0.0	+WY	+	++YG	++	++	++
	1.4	++YG	++	+++	+++	+++	+++
	2.2	++YG	+++	+++	+++	+++	+++
	4.0	+YG	++	++	++	++	++
3. *A. niger*	0.0	+B	+	+	+	+	+
	1.5	++B	++	+++	+++	+++	+++
	2.3	++B	++	++	++	++	++
	4.5	+B	++	++	++	++	++
4. *H. cladosporioides*	0.0	++G	+++	+++	+++	+++	+++
	1.6	+G	++	++	++	++	++
	2.7	+G	++	++	++	++	++
	3.3	+G	+	+	+	+	+
5. *M. sylvaticus* ...	0.0	+W	++	++	++	++	++
	1.1	—	—	—	—	—	—
	2.3	—	—	—	—	—	—
	3.5	—	—	—	—	—	—
6. *O. lactis var. A.*	0.0	—	—	—	—	—	—
	1.4	—	—	—	—	—	—
	1.6	—	—	—	—	—	—
	3.0	—	—	—	—	—	—
7. *O. lactis var. B.*	0.0	—	—	—	—	—	—
	0.9	—	—	—	—	—	—
	2.1	—	—	—	—	—	—
	3.1	—	—	—	—	—	—
8. *P. biforme*	0.0	+W	+	+	+	+	+
	0.7	—	—	—	—	—	—
	2.3	+WG	+G	+	+	+	+
	3.1	—	+G	+	+	+	+
9. *P. expansum* ...	0.0	+G	++	++	++	++	++
	1.3	+G	++	++	++	++	++
	2.2	+G	++	++	++	++	++
	3.0	+G	+	+	+	+	+
10. *R. nigricans* ...	0.0	—	—	—	—	—	—
	1.3	—	—	—	—	—	—
	2.1	—	—	—	—	—	—
	4.0	—	—	—	—	—	—
Check	0.0	—	—	—	—	—	—

and mineral salts and the materials related to them furnish the great variety of essential elements for microbiological activity. Butter is a substance consisting principally of a mixture of fats that carry a rich supply of carbon, oxygen, and hydrogen. Held within this mass of fat are droplets of material consisting of such substances as the proteins, casein and albumin, the carbohydrate lactose, a variety of mineral salts, and by-products of the decomposition of any of these compounds, all in association with a relatively large amount of water.

It seemed desirable that a study should be made of the relative value of the various constituents of butter as foods for molds, specifically for cultures that were selected as representative of the species commonly found in butter. (See p. 22.) As fat is the principal constituent of butter, it was made the subject of the first trials. It is generally agreed that fat is not the most desirable food for microörganisms. This does not mean, however, that all forms fail to utilize the various glycerides. While it is not easy to obtain fat in an absolutely pure state, it is possible to purify it with reasonable success without altering its character appreciably. As reported in previous pages, the species of molds studied did not make significant growth on purified butterfat unless some water was present. This is reasonable, as a certain amount of water is necessary for any biological process involving the metabolism of living protoplasm. When growth was obtained on the butterfat to which water had been added, there was a possibility that it was due to other substances present as impurities in the fat. At any rate, development was not extensive under these conditions and altho germination of conidia occurred in some cases, the amount of mycelium formed was seldom great. Microscopic studies showed that in some instances initial development occurred but was soon checked and followed by a disintegration of the hyphae. The slight development on purified fats might well be attributed to a supply of nutrients within the inoculum, and present in such minute quantities that growth was soon impossible. The trials with butterfat obtained from various sources and treated in different ways did not show any particular advantage of one type of butterfat over another. None of them were to be considered as very satisfactory direct sources of food for the early development of the molds being studied, even when water was present to improve the opportunities for growth. These results are in line with previous investigations and in accordance with the observation that butter oils seldom are affected with mold growth.

Lecithin, which contains nitrogen and phosphorus in addition to carbon, hydrogen, and oxygen, is known to exist in butter. When this substance, obtained from dried buttermilk and in a highly purified condition, was emulsified in water and inoculated with the experimental cultures, growth was observed in every case. In this preparation some of the cultures developed only in the depth of the liquid, but the species that produce the most extensive growth on butter developed reasonably well on the surface. When a solid substrate was afforded the cultures, the growth was much more marked.

Everyone familiar with the butter industry appreciates that molding most often occurs after butter has been stored for a time. During this time the fats may be hydrolyzed so that glycerol and the constituent acids are released. In this connection, it was desirable to consider the value of glycerol and some of the organic acids commonly present in the mixed glycerides known as fat. It was found that glycerol was not a particularly favorable source of food for the cultures used, at least in the concentration employed. Development below the surface, in almost every instance, was much better than that on the surface of the medium, whether the glycerol was in a liquid or a solid medium. Butyric acid was the only water-soluble fatty acid studied. In the one per cent aqueous solution of this common hydrolytic product of butterfat, growth was not observed in any instance. Apparently it was toxic for the cultures studied. The growth in the unsaturated oleic acid was much better than that obtained on the saturated palmitic acid, which in turn appeared to be more nearly suited to the demands of the molds studied than the other typical saturated fatty acid, stearic. As oleic acid predominates in butterfat, on some occasions it may be called upon to furnish the food supply of molds.

In a general way butterfat, lecithin, and related substances, were not particularly satisfactory sources of food for the early development of the conidia of the mold cultures used. Normal growth was not obtained in any of these substances, even where sufficient quantities of water were present. It is conceivable, however, that these compounds may be utilized readily by molds that have made their early development of mycelium upon substrata furnishing more suitable food supplies, and after the enzymes necessary to split the fats into readily assimilable compounds have been formed. Many of the typical flavors and odors produced in butter and cheese, such as those characteristic of Roquefort cheese, are associated with fat hydrolysis by molds. Such a flavor and aroma was noticeable in some of the fat, water, and agar combinations before there were any visible signs of mycelium. This hydrolysis of the fat may have been the result of enzymes carried by the inoculum, but it is possible that the germinated hyphae produced enzymes when they were called upon to supply nourishment, with fat as the only available source of food. Fat and its related compounds must be considered as potential sources of food for mold growth.

Nitrogen is one of the most important of the elements for the metabolism of the living cell. Many nitrogen-bearing compounds are suitable for this purpose but natural proteins, their split products (peptone, amino acids, etc.), and related compounds are generally considered the most satisfactory sources of nitrogen for microörganisms. Organisms that can obtain their nitrogen directly from the atmosphere as elementary nitrogen, are known but the species under investigation have not been shown capable of fixing nitrogen in this manner. Rather, they must use other sources of supply. The part of butter that furnishes nitrogen compounds in considerable amounts is known as the curd. This is really a misnomer, as casein, albumin, and similar nitrogenous complexes normally found in milk are carried over into the butter in much the same form as they exist in milk, or more correctly, in buttermilk. This buttermilk is held in butter principally in the form of tiny droplets, with a full quota of the water, which makes up the bulk of buttermilk. As a starting point in the investigation of the value of nitrogenous substances as a source of food for molds, solutions of peptone were used. The germination and hyphal development of the cultures on this substrate were both rapid and luxuriant, and growth was as extensive as might be desired. In contrast with the tendency toward subsurface development in the fatty substances, the growth on peptone was predominately on the surface. The more noticeable surface development of the cultures upon lecithin preparations than upon fats or fatty acids may be due to a nitrogen-bearing radical in the lecithin molecule.

In order to obtain an idea of the usefulness of the actual curd portion of butter for the growth of molds, the fat was removed from a sample of typical butter so that the curd and water portion became available. (See page 35.) This substance consisted of a mixture of casein, albumin, lactose, and mineral salts, with about 85 per cent of water. The growth of the test cultures on this substrate was prompt and luxuriant. When this material was dialyzed to remove some of the soluble constituents, such as lactose, mineral salts, and other diffusible compounds, the residue served adequately as a source of food for the molds being studied. While growth was not quite so rapid as upon the original mixture, it became equally extensive in a short time. This demonstrated that the important constituents were not diffused through a collodion membrane and indicated that the principal sources of subsistence were the colloidal compounds of nitrogen.

As a further test of the non-fatty portions of butter, which were to be considered as largely nitrogenous, from the theoretical standpoint at least, the sera obtained from the successive washings and separations of cream (see page 36) were employed as substrata for the cultures. The first washings were found to be satisfactory sources of nutrients but each successive washing left less and less material for the needs of a growing cell. This may be considered to indicate that a rich source of food is incorporated in butter in the form of the solids-not-fat in cream and that the purification of fat by successive washings and separations may remove so much of the food for fungi that growth would be materially retarded in the finished product consisting largely of fat. Preliminary studies now under way lead the writer to believe that this is actually the case.

As lactose is a constituent of butter, an investigation was undertaken to determine its suitability as a food for the experimental cultures. In an aqueous solution of lactose, growth was very meager, especially on the surface. Some subsurface mycelial development was noted, especially in the bottom of the liquid. When the lactose was held in a washed agar medium, growth was somewhat better, especially in the depth of the agar. A penetration of the substrate occurred with all cultures. The species of Hormodendrum and Alternaria grew luxuriantly below the surface and carried a deep green and almost black color in their mycelia; very scanty growth appeared on the surface.

Lactic acid, which is so commonly formed by the fermentation of lactose, did not prove a satisfactory food source and, in general, growth of the molds studied was poor at the concentration used.

The diffusate obtained by the dialysis of the curd of butter was a much more satisfactory substrate than pure lactose solutions. This may be attributed to the presence of soluble nitrogen compounds and mineral salts in addition to lactose. At any rate, with the diffusate the growth was limited almost entirely to the surface of the liquid, which is suggestive of the results obtained with nitrogenous substances. Development was most active within a few days, and continued incubation did not significantly increase the visible mycelium. This indicates an early exhaustion of essential food elements. The belief that nitrogen compounds are the principal sources of nourishment was substantiated in part by an observation on the pH of the substrate in different cultures. The initial pH of the diffusate was 6.4. After 3 weeks the hydrogen-ion concentration of the medium seeded with Cultures 6 and 7, which developed the least, was pH 6.2 in each case. In the other cultures, the reaction was altered to points from pH 7.0 to 7.6, which was suggestive of alkaline by-products of protein hydrolysis.

Lactose was not satisfactory material for the growth of the test cultures. The more abundant growth in the depth of the medium was in accordance with a similar phenomenon in the case of substrata containing glycerol, fatty acids, and fats, all of which are compounds lacking nitrogen. The fact that subsurface growth was also noticeable in the non-nutritive washed agar medium, which served as a check, might indicate that where the food supply was not especially favorable the tendency was toward deeper penetration of the substrate. This is not an entirely satisfactory explanation, however. The species of Hormodendrum and Alternaria showed a tendency to spread into the depth of butter, much as they did on the above-mentioned media, and produced similar dark-colored mycelium even when an adequate and desirable food supply was available. Some reason other than the lack of suitable food must be sought to explain this situation.

Almost everyone will concede that mineral elements of various sorts are essential for the growth of microörganisms. Fortunately, minute traces are ordinarily sufficient to meet the needs of the living cell. In a natural product like milk, they usually exist in combination with other constituents or as impurities, even after attempted purifications. Molds would not be expected to grow in such a highly alkaline preparation as a solution of milk ash. The results presented demonstrate this. However, a 0.75 per cent solution was not sufficient to destroy the conidia, as evidenced by the fact that they were capable of normal growth when sources of nitrogen, carbon, etc., were supplied. It is surprising that growth occurred in such an ash solution even when it was neutralized, as theoretically no nitrogen or carbon was present. These elements might have been supplied from some other source when molds were able to grow in a neutralized ash solution.

Growth of the cultures in mixtures of butterfat, lecithin, and water was not conspicuous. The surface tension may be a factor in this, as both of the former substances depress the surface tension, the combination perhaps more than either alone. The presence of particles of milk ash on butterfat, in an environment well supplied with water, appeared to encourage the development of certain species but could not be considered as giving good growth. When the solutions of ash were mixed more intimately with the fat, the growth was much better. This probably means that the mineral salts added a stimulus for the attack upon fat.

The results with a combination of peptone and lactose in liquid or solid media indicated how important is a nitrogenous compound for the development of fungi. While the proportion of growth on the surface of the medium was much greater than on simple lactose substrata, there was a greater tendency for subsurface mycelium to develop than in pure peptone solutions. This may mean that there is something fundamental about the mode of development of molds upon nitrogenous and non-nitrogenous media. The disturbance in the normal surface development of molds in the presence of such substances as lactose, glycerol, fatty acids, and fat is striking.

Altogether, butter provides a wide variety of foodstuffs, quite sufficient to sustain the growth of molds. The important consideration is not the amount or quality of the food, however, but its availability. The physical structure of butter must be taken into account, as the most desirable nutrients are dispersed in minute droplets throughout the mass of fat. If the molds happen to be situated where this food is accessible, and if other factors are favorable, growth should take place freely.

Moisture.—The effect of moisture on the growth of molds is clear. All living protoplasm has a relatively high moisture content and the normal nutrition of the cell takes place from a food supply dispersed in an aqueous dispersion medium.

Moisture-free fat is not a good substrate for growth. Butter regularly carries a reasonable amount of moisture even upon a basis of percentage total composition. When it is borne in mind that butter is more than 80 per cent fat, and that the water, constituting from 12 to 16 per cent of the total weight, is largely in association with the nitrogenous compounds as well as the lactose, mineral salts, and various traces of other compounds, in the form of buttermilk droplets, it may be appreciated that there should be a plentiful supply of moisture for the growth of molds. It has already been pointed out that by actual analysis the curd portion of butter was about 85 per cent water. Therefore it may be assumed with reasonable assurance of correctness that the moisture conditions in normal butter are perfectly satisfactory.

The humidity of the atmosphere, however, is not such a constant factor, especially in relation to the outer surface of butter. Sometimes butter is stored in a dry, well-ventilated refrigerator, or again in a damp place where the air is stagnant and evaporation slight so that the moisture on the surface of the butter is retained. The results of the experiments reported in preceding pages indicate that humidity may play a considerable part in the development of molds on butter. There is a significant fact which stands out in this connection, however. It appeared that sterile butter, inoculated on the surface with mold spores, failed to show any mold growth when kept in a storage room at a low humidity but extensive growth took place when the atmosphere was saturated with moisture. On the other hand, butter made from cream in which molds had been growing for several days developed moldy areas even under conditions of low humidity. Apparently a fundamental difference is involved. In the first lot of butter the conidia found it difficult or impossible to germinate because of the lack of moisture brought about by evaporation on the surface; in butter in which molds were growing actively, the process was checked only temporarily during churning and continued afterwards because of the abundant supply of moisture obtained through the mycelium from the reservoirs of water in the droplets of buttermilk. This feature may be of practical significance. If infection takes place before churning and the molds are able to establish a mycelial development before the butter is made, growth may continue and the surface of the butter be marred in appearance, even tho the product be stored in an atmosphere low in moisture and conducive to rapid evaporation. On the other hand, if contamination takes place after the butter is made, and the finished product is kept at a low humidity, mold may not appear. Undoubtedly, a dry, well-ventilated storage room may be an important factor in preventing the molding of butter.

Temperature.—The temperature at which mold growth occurs varies decidedly with the species of molds and the nature of the substrate. The results of the experiments reported demonstrate clearly that *Aspergillus niger*, and *Aspergillus flavus* were checked when the temperature of incubation was below 10° C. This indicates that these species need not be considered as responsible for the discoloration of butter as long as the product is kept at low temperatures. The growth of *Rhizopus nigricans* was inhibited at a temperature of 0° C. Species of Penicillium, Alternaria, and Hormodendrum were not so sensitive to low temperatures. This is significant, as these species are among the most common causes of molding in butter, even when it is kept at low temperature. The amount of salt in the butter also affected the growth of the various species at different temperatures. It had a more noticeable effect on the growth of the molds at low than at high temperatures. Time is a very important factor in the growth at lower temperatures. As might be expected, species which are able to grow at low temperatures may require considerable time before they can produce noticeable growth, also the species that are least inhibited by salt grow at the lower temperatures. As the amount of salt in the butter has a marked effect upon the freezing point of the water droplets containing the food materials, with a high salt content the nutrients may remain in a liquid substrate at temperatures much below the ordinary freezing point of water. Consequently, species able to grow at low temperatures and at high salt concentrations may bring about the molding of butter in storage if time is allowed for their growth. The temperatures used in these studies were not especially low, so it would be desirable to continue the investigations at much lower temperatures with species known to be common causes of molding in butter.

Atmosphere.—The effect of atmospheric conditions, aside from humidity, upon the growth of molds, is worth consideration. The results of the experiments reported here indicate that a sufficient supply of oxygen is essential for the development of the ordinary molds. When the amount of available oxygen was reduced by a partial evacuation of the air within a sealed container in which infected butter was stored, the growth was retarded but, in time, development began. It is possible that oxygen was released from the food constituents after the atmospheric oxygen was consumed and eventually permitted satisfactory growth of most of the species studied. Where the oxygen was removed so that anaerobic conditions existed, no growth of molds occurred. Butter is seldom stored where oxygen is completely excluded. Sometimes it is placed in containers upon which a partial vacuum is drawn. Consequently, under ordinary commercial conditions, the supply of oxygen may be considered reasonably satisfactory.

In sealed containers, mold growth may appear, as it sometimes does in canned condensed milk. This condition was studied in the experiment in which butter was kept in a partial vacuum. It is not economically feasible, however, to handle butter where all oxygen is removed. It may be possible to replace the oxygen by some inert gas, but experiments are necessary to demonstrate the practicability of such a plan. The partial removal of carbon dioxide from the atmosphere in which butter was stored did not retard mold development in the experimental samples. How essential carbon dioxide is for mold growth has not been determined, but further studies should be made to ascertain this point. Without doubt, atmospheric conditions influence mold development, but to what extent is not yet evident. The fact that certain species were able to grow so extensively in the depth of media containing carbohydrates, fatty acids, glycerol, etc., raises a question as to these relationships.

Salt.—The amount of salt in butter is unquestionably an important factor influencing the growth of molds. The results presented in the foregoing pages demonstrate that the effect of salt upon growth depends especially upon the species of molds, the amount of moisture, and the temperature. In accordance with many previous investigations, *Oospora lactis* was checked by a slight concentration of sodium chloride in the substrate. The disappearance of this fungus in salted butter may be explained on this basis. The species of Mucor and Rhizopus studied were only slightly more resistant to salt and consequently would not be expected to be important in the molding of salted butter. *Aspergillus niger* and *Aspergillus flavus* are resistant to high salt concentrations, but when butter was kept at temperatures below 10° C. growth was impeded. For this reason, their importance as causes of molding in butter stored at the usual commercial temperatures is slight. The other molds studied—Alternaria, Hormodendrum, and Penicillium—were found to be capable of growing in high salt concentrations and at the lower temperatures. As these species produce the most marked changes in the appearance, flavor, and aroma of butter when they are able to develop, they are of major importance. The species of Alternaria and Hormodendrum studied produced dark green, almost black, smudgy areas. Their mycelia spread considerable distances from the point of infection, both along the surface and to considerable depths in the butter. The species of Penicillium used did not mar the appearance of the butter particularly, altho in some cases sufficient green fruiting bodies were formed to give a slight, dusty discoloration of the surface. The cultures of Penicillium affected largely the flavor and aroma. Butters in which these species were growing became distinctly cheesy in flavor and odor, and in these characters suggested Roquefort cheese. In any consideration of the effect of salt on the growth of mold in butter, the concentration of the salt in the droplets of water within the butter must be taken into account. Even tho a gravimetric analysis of butter may indicate a high salt content, it is important to know how much water is present to carry this salt. Some of the experiments reported in the preceding pages illustrate this point. If the percentages of water and salt are both high, the concentration of salt in the water may not be any higher than if both are low. Equally, if the water content is low and the salt content moderately high, the brine may be highly concentrated. Then, also, the salt may be unevenly distributed in the minute droplets of moisture within the butter. Some may represent a strong and others a weak brine. The number of conidia in butter, even under extreme conditions, will seldom be large and never considerable in proportion to the number of water droplets. It is conceivable that a conidium may be allocated to a droplet of water containing little or no salt and an abundant supply of food and accordingly be able to germinate and develop without restraint. Only one such instance would lead to serious consequences as far as molding is concerned. Thus the effect of salt on the growth of mold on butter will depend entirely upon the relative concentration of the salt in the droplets in which the mold spores, or mycelium, may be located. This may partly explain the molding of salted butter, even tho the composition of the butter and type of mold may at first have been considered sufficient reasons for expecting protection against such a contingency.

Species of molds.—It is clearly evident that the species of molds must be considered as factors in the molding of butter. A wide variety of species has been isolated from butter. Among these, the ten selected for the studies reported were all capable of growing in butter under favorable conditions. From the standpoint of visible growth, *Oospora lactis* was least noticeable. It seldom appeared on the surface of the inoculated butter but evidently was able to develop in unsalted butter, as shown by the fact that in nearly every instance the odor of the butter became distinctly cheesy, resembling most closely the odor of Cheddar or Brick cheese. *Aspergillus flavus* produced a slight, white felt upon the butter and also fruited extensively to produce yellow or yellowish-green sporangia above the surface of the butter. It produced a rather indefinite change in the aroma of the butter that was suggestive of fat hydrolysis and bordered on that produced in Roquefort cheese. *Aspergillus niger* likewise formed a white, cottony layer of mycelium from which a large number of chocolate-brown or black sporangia arose. The odor produced in the butter was much the same as that observed with *Aspergillus flavus*. *Alternaria humicola* grew extensively in the form of a white, surface mycelium that eventually became dark green, and penetrated into the butter to cause a very dark green or black smudge. The odor produced was peculiar, with a suggestion of acetic and butyric acids as well as a slight cheesiness, resembling a rather poor quality of Cheddar. *Hormodendrum cladosporioides* grew rapidly and extensively, producing dark green fruiting bodies promptly and sending dark green or black hyphae into the butter and spreading widely over the surface. The principal change in the odor of the butter was the development of mustiness, with a faint suggestion of the aroma of an old cottage cheese. *Mucor sylvaticus* sent up an extensive aerial mycelium terminating in numerous grayish or black sporangia. The odor of the butter was rather indefinite but resembled acetic and butyric acids, and also suggested tallow. *Penicillium expansum* and *Penicillium biforme* produced white, cushion-like spots which, in time, became gray-green to blue-green. The aroma of both species was decidedly like that of Roquefort cheese, altho some other indefinable odors were noticeable. The observation that the Penicillium species were capable of producing the characteristic odor of Roquefort cheese in butterfat and butter when there were no visible signs of growth deserves mention. In a similar way, other molds may bring about alterations in the flavor or aroma of butter without affecting the appearance. *Rhizopus nigricans* grew well on the unsalted butter and appeared as a mass of aerial mycelium topped with many black sporangia. The odor was not markedly affected altho a slight acetic acid aroma appeared in time. As may be seen, most of the mold species studied grew well in butter when humidity, temperature, atmosphere, and salt concentration were favorable, and produced evident changes in the appearance and odor of the butter. The other species of molds isolated should be studied in a similar manner, to determine which can actually grow in butter and, if growth is possible, what conditions influence the development.

It is evident that, qualitatively and quantitatively, butter contains a satisfactory supply of food for mold growth. Whether or not molds will develop upon a given lot of butter depends upon several factors, among which must be considered, especially, the extent of contamination, the species of molds, the supply of oxygen, the temperature, and the concentration of salt in the aqueous portion of the butter carrying the major portion of the most useful food constituents. A great deal of work remains to be done to elucidate some of these points.

SUMMARY

1. Studies were made of some of the factors influencing the growth of molds in butter.

2. The ten species of molds isolated from butter and selected for the investigations, were as follows: *Alternaria humicola, Aspergillus flavus, Aspergillus niger, Hormodendrum cladosporioides, Mucor syl-*

vaticus, Oospora lactis var. A., Oospora lactis var. B., Penicillium biforme, Penicillium expansum, and *Rhizopus nigricans.*

3. The influence of the food supply, moisture, atmosphere, temperature, and salt concentration upon the growth of the ten species was studied.

4. Purified butterfat was not a readily utilizable food, unless water was present. In that case, growth was only moderate, however.

5. Lecithin proved to be a reasonably satisfactory food for the molds studied.

6. The hydrolytic products of fat that provided fairly satisfactory nutriment were glycerol, palmitic acid, and oleic acid. *Alternaria humicola* made slight growth on media containing stearic acid as the only source of food. No growth occurred on a one per cent solution of butyric acid.

7. Compounds containing nitrogen, such as peptone, curd from butter, and serum from cream, were found to be excellent sources of food. Growth was luxuriant on the substrata containing these nitrogenous substances.

8. Lactose and lactic acid in one per cent solutions did not furnish especially good nutriment.

9. Solutions of milk ash were not readily utilized by the molds studied unless they were neutralized.

10. Combinations of fat, lecithin, and water; fat and ash; fat, ash, and water; and lactose and peptone, provided far better growth than was obtained on the single substances.

11. The molds grew most extensively on the surfaces of media containing nitrogen-bearing compounds.

12. The growth on substrata containing fats, fatty acids, glycerol, lactose, or lactic acid was largely below the surface of the medium.

13. Unsalted butter containing a mixture of fat, protein, carbohydrate, and ash supported active growth.

14. The humidity of the atmosphere had a marked influence upon the growth of the molds on butter, especially when the surface of the butter was contaminated. At low humidities growth was checked. When the molds were actively growing in the cream before the butter was made, the humidity had a less pronounced effect upon the growth.

15. Temperature exerted a marked influence upon the growth of the species in various substrata. Growth was active in all at 20° to 25° C. *Aspergillus flavus* was checked at a temperature of 10° C. or lower; *Aspergillus niger* and *Rhizopus nigricans* at 0° C. *Mucor sylvaticus* grew in whey media and buttermilk, but not in butter kept at 0°. The other species were able to develop at 0° C. but the growth was not so extensive or so rapid as that at 10° and 20° C. Time is a factor influencing the growth at low temperatures.

16. The species of molds studied were able to grow on butter at 20° to 25° C. when under a vacuum of 25 inches.

17. Partially removing carbon dioxide from the atmosphere did not prevent the growth of the molds on butter.

18. None of the molds were able to develop when the oxygen was exhausted from the atmosphere.

19. Salt exerted a marked effect upon the growth of certain species.

20. *Oospora lactis*, *Mucor sylvaticus*, and *Rhizopus nigricans* were most readily affected and their growth was inhibited when the concentration of salt exceeded 5 per cent.

21. *Alternaria humicola*, *Aspergillus flavus*, *Aspergillus niger*, *Hormodendrum cladosporioides*, *Penicillium biforme*, and *Penicillium expansum* were capable of growing in media containing 15 per cent of salt. In some cases, the species of Penicillium showed slight growth when the percentage was as high as 20 per cent.

22. The extent to which salt inhibited the growth of the molds studied depended upon the species of molds, and the temperature of incubation.

23. All the species of molds studied were able to grow on butter when conditions were favorable.

24. The appearance of the butter was marred most extensively by *Alternaria humicola* and *Hormodendrum cladosporioides*. The flavor and odor of the butter were affected seriously by all the other species.

25. As an ample food and water supply are provided, the growth of molds in butter appears to depend largely upon the species of mold, the humidity of the atmosphere, the supply of oxygen, the temperature of storage, time, and the concentration of salt. These influences may act separately or collectively.

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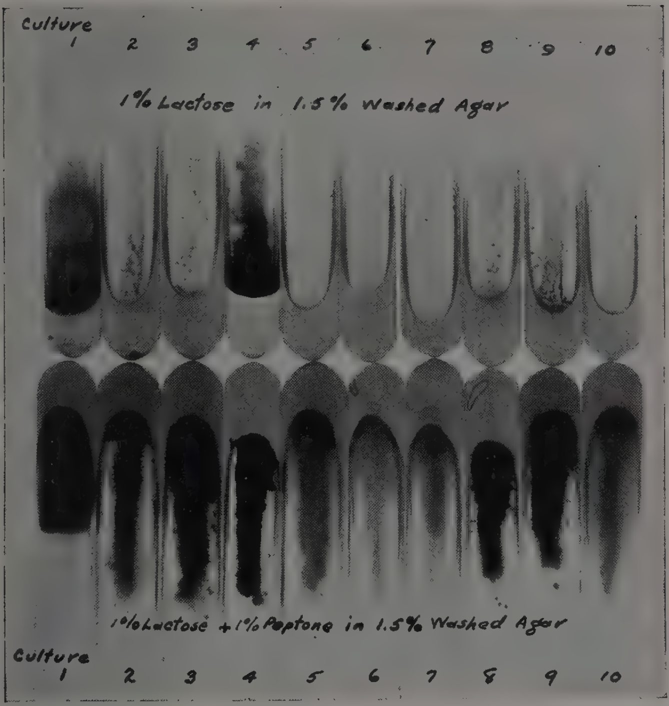
Culture
1 2 3 4 5 6 7 8 9 10
1% Lactose in 1.5% Washed Agar
1% Lactose + 1% Peptone in 1.5% Washed Agar
Culture
1 2 3 4 5 6 7 8 9 10

Plate I. Comparative Growth of Test Cultures on One Per Cent Lactose in 1.5 Per Cent Washed Agar and on One Per Cent Lactose + One Per Cent Peptone in 1.5 Per Cent Washed Agar

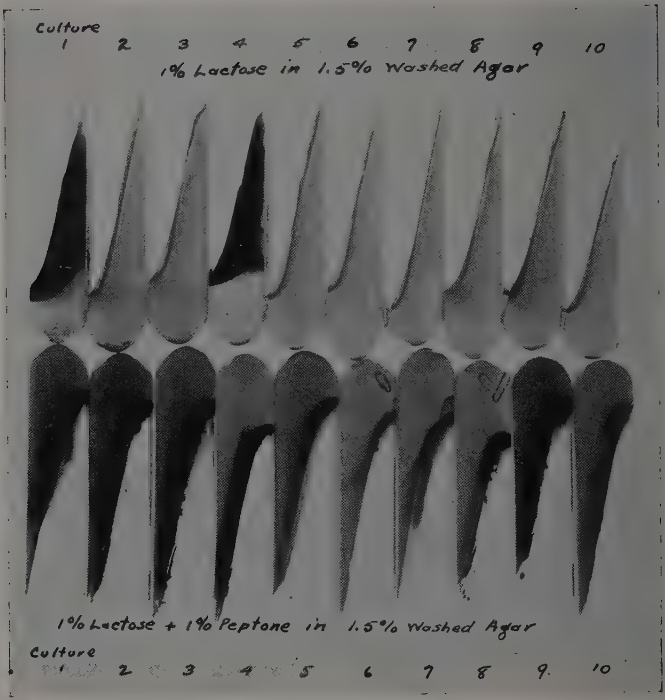
Culture
1 2 3 4 5 6 7 8 9 10
1% Lactose in 1.5% Washed Agar
1% Lactose + 1% Peptone in 1.5% Washed Agar
Culture
1 2 3 4 5 6 7 8 9 10

Plate 2. Penetration of Mycelium into Substrate

The apparent clouding in the medium containing lactose and peptone together is due largely to shadows cast from the surface mycelium.

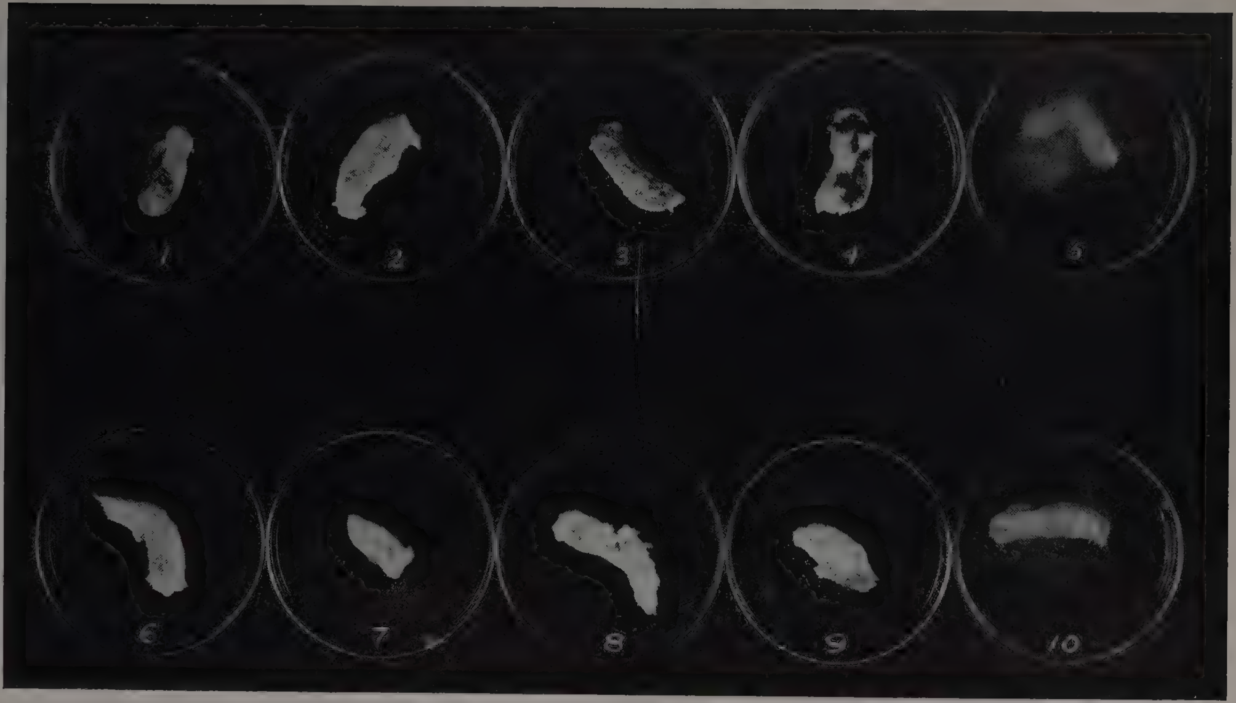

Plate 3. Typical Appearance of Growth of Test Cultures on Unsalted Butter

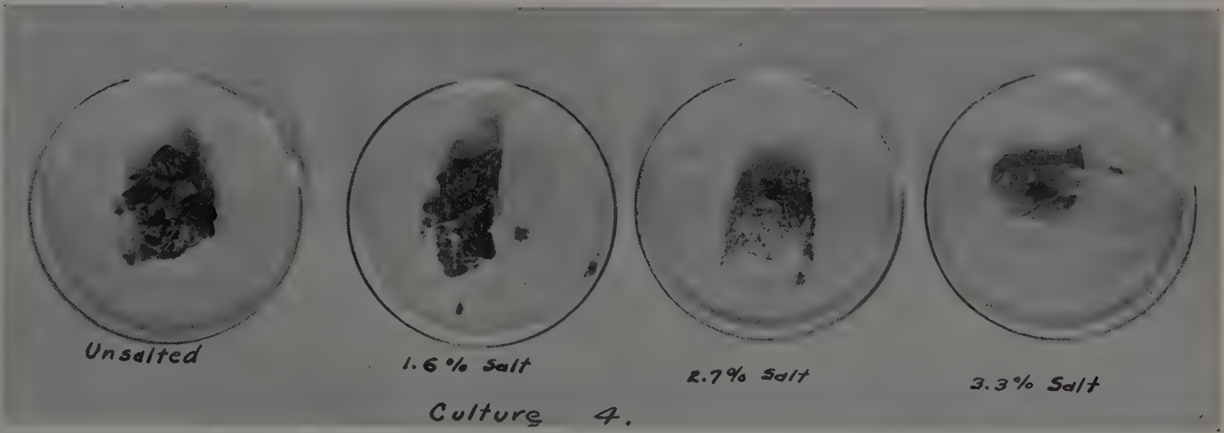

Plate 4. Effect of Salt Concentration upon the Growth of *Hormodendrum cladosporioides* in Butter

Technical Bulletin 65 December 1929

University of Minnesota
Agricultural Experiment Station

Mutation and Hybridization in Ustilago Zeae

PART I. MUTATION

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PART II. HYBRIDIZATION

J. J. Christensen
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CONTENTS

Part I. Mutation

Page

Introduction 3

Previous work 5

Materials and methods 5

How mutants arise 7

Frequency of mutation 8

Mutant characters 14
  General cultural characters 14
    General statement 14
    Type of growth 16
    Consistency of colonies 16
    Direction of growth 18
    Size of colonies 19
    Elevation of colonies 23
    Color of colonies 23
    Surface characters of colonies 24
  Physiologic characters 25
    General statement 25
    Growth on standard bacteriologic media 27
    Digestion of casein 30
    Effect on sugars 31
    Reduction of nitrates and iodine 31
    Temperature relations 33
  Morphology of sporidia 35
  Pathogenicity and sex 36

Factors affecting mutation 43
  Nutrients 44
  Temperature 46
  Light 47

Degree of constancy of mutant characters 47

Does true mutation occur in *Ustilago zeae?* 53

Significance of mutation 61

Summary 63

Literature cited 64

Plates 67

Part II. Hybridization

Introduction 89

Are there "geographic strains"? 89

Terminology 91

Crosses made for study of f_1 lines 92

Characters of f_1 lines 93
  Sexual characters 93
  Further experiments with lines that caused infection singly 97
  Cultural characters 99
  Mutability 102
  Pathogenicity 102

Conclusions 105

Summary 106

Literature cited 107

Plates 109

MUTATION AND HYBRIDIZATION IN USTILAGO ZEAE[1]

Part 1. Mutation

E. C. Stakman, J. J. Christensen, C. J. Eide, and Bjorn Peturson[2]

INTRODUCTION

Ustilago zeae (Beckm.) Ung. comprises an indefinite number of unisexual lines that differ in so many physiologic characters that it seems justifiable to consider them physiologic forms (44, 45). It seems scarcely necessary to point out the importance of an intimate knowledge of physiologic specialization of plant pathogenes. A clear concept of the implications of the phenomenon is especially important in taxonomic work, in epidemiology studies, in establishing plant quarantines, and in breeding disease-resistant varieties of crop plants (8, 43). But it is important not only to know the number, pathogenic capabilities, and geographic distribution of forms now in existence but also to learn how commonly new forms are coming into being. The more precisely we can know what to expect, the more intelligently we can act.

We know that corn smut is a destructive disease that can be controlled adequately only by using resistant varieties, and we know that such varieties can be produced (26, 30). But we know also that there are many physiologic forms of *U. zeae,* the pathogene causing most of the smut in the corn belt of the United States, and that selfed lines of corn may be resistant to some combinations of forms and susceptible to others (15). Assuming that some lines are resistant to all existing smut forms, it would be highly desirable to know whether new forms might arise to which they would be susceptible. This, then, raises the question as to the genetic stability of physiologic forms.

Contrary to the older belief that differences between physiologic forms of many fungi are only phenotypic, there is abundant evidence that they are genotypic. The idea that forms change readily by a process of education or adaptation has been disproved to a considerable extent (43). This does not mean that new forms may not appear but that physiologic forms of fungi probably are not unique genetically. Their physiologic and parasitic characters are due to the interaction of genetic and environmental factors, as are the characters of higher plants. Consequently the laws of inheritance apply in both cases. There seems to be no valid reason, then, for supposing that new physiologic forms originate otherwise than by hybridization and mutation. That they probably arise in both these ways in *U. zeae* has been shown by Christensen and Stakman (15); Stakman and Christensen (44); Stakman, Christensen, and Hanna (45); and Hanna (24). But how often and under what circumstances they arise and what their pathogenic capabilities are after they have arisen is only imperfectly known. The writers have attempted an extensive study of physiologic specialization in *U. zeae,* because of its practical importance and because this species is very suitable for a study of the nature and origin of physiologic forms.

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[1] This manuscript was submitted for publication in October, 1929.

[2] The writers are greatly indebted to numerous pathologists and agronomists in the United States and to Dr. Bela Husz of Hungary, Dr. E. Pantanelli of Italy, Dr. Louis M. Unamuno Yrigoyen of Spain, and Dr. J. Dufrenoy of France, for collections of corn smut. They are also indebted to Dr. W. F. Hanna for certain monosporidial isolations and to R. H. Bamberg and C. S. Holton for assistance in making monosporidial isolations and inoculations.

The mature chlamydospores of *U. zeae* are diploid. On germination they normally produce a promycelium in which reduction division apparently occurs (24). The sporidia typically are uninucleate, altho they sometimes contain more than one nucleus, and the progeny of a single sporidium should constitute a clonal line, as it buds in a yeast-like manner and thus multiplies indefinitely by vegetative propagation. These haploid or gametic clonal lines grow readily in artificial culture, and single sporidia can be isolated easily; hence studies of mutation can be made under unusually favorable circumstances. Furthermore, *U. zeae* usually is heterothallic, sexual fusions being prerequisite to normal infection in most cases (19, 24, 44). There is a relatively short dikaryophase, followed by nuclear fusion and formation of the diploid chlamydospores. These chlamydospores usually are produced about two weeks after the plants are inoculated, and they germinate readily; consequently only a short time is required for hybridization studies.

But there are difficulties in determining the pathogenicity of the new physiologic forms that arise by mutation and hybridization. Most monosporidial lines alone cannot cause normal infection. They represent the saprogenic phase in the life history of the pathogene. Moreover, the dikaryophytes and diplonts apparently cannot be produced on artificial culture media, but only in the living host. Therefore it is necessary to determine the pathogenicity of combinations of forms, as that of the individuals alone cannot be determined. This condition in the smuts is somewhat unique, being quite different from that in most other pathogenic fungi, in which individual monosporous lines can cause infection.[3]

It was the object of the present investigation to study the genetic stability of *U. zeae* to obtain facts of value in the solution of the corn smut problem, and particularly to learn as much as possible about the general problem of the origin, nature, and importance of physiologic forms of pathogenic fungi. About 200 monosporidial lines of *U. zeae* have been studied more or less intensively, particularly with reference to mutation and hybridization.

---

[3] While this manuscript was being prepared, evidence was obtained by one of the authors (Christensen) that some monospordial lines could cause infection when inoculated singly into corn plants. The results are presented in Part II.

PREVIOUS WORK

Kniep (31, 32) and Zillig (47), in their investigations of *Ustilago violacea* (Pers.) Fuck., called attention to the gametic nature of sporidia and thus laid the foundation for studies of hybridization and mutation in the Ustilaginales.

Bauch (1), in 1925, was the first to record mutation in the smut fungi. He observed the phenomenon in *Ustilago bromivora* (Tul.) F. de W. Christensen and Stakman (15), Stakman, Christensen, and Hanna (45), and Hanna (24) demonstrated that mutation is very common in *U. zeae*. Stakman, Christensen, and Hanna stated that a very large number of mutants might arise from monosporidial lines, which they consider haploid clones. They pointed out that the mutants might differ consistently from their parents and from each other in one or more of the following respects: morphology, cultural characters, and apparently sometimes in sex and potential pathogenicity. According to these authors, the frequency of mutation can be influenced by certain environmental conditions, altho suitable media often are necessary to bring out the differences between mutants.

Part I of this bulletin records the data on mutation obtained by the writers during the past two years, and Part II gives the results of studies on hybridization.

MATERIALS AND METHODS

More than 200 monosporidial lines of *U. zeae* were isolated and observed to some extent in the study of mutation. The method of isolating sporidia was that described by Hanna (23). In some cases the individual sporidia were isolated directly from the promycelium, in others shortly after the sporidia had become detached, and in still others from cultures of smut lines that had been grown for many months, or, in some cases, years.

The collections from which these monosporidial lines were derived were obtained from many different localities in the United States, from Canada, and from Hungary, Italy, France, and Spain. When cultures were made from collections of chlamydospores, the spores were soaked for twenty-four hours or longer in a 1 per cent copper sulfate solution and then used either for pouring dilution plates or for making streak inoculations on agar. The individual sporidia were then isolated from the cultures.

Monosporidial lines are designated by the locality from which they were obtained. If several distinct lines were isolated from a promycelium, locality, or collection, each was given a letter of the alphabet. Thus Minn. A, Minn. B, Minn. C, and Minn. D were isolated from the same promycelium of a chlamydospore from a Minnesota collection. The chlamydospores of an Italian collection received from Dr. Pantanelli were plated out by the dilution method, and there were several types of resulting colonies. Transfers were made from them, and it was evident that there were several distinct cultural types. These lines were designated Italy A, Italy B, Italy C, Italy D, etc. Again, Dr. R. J. Garber sent three packets of chlamydospores from West Virginia, labeled "leaf strain," "basal strain," and "ear strain," indicating the region of the plant on which the galls had been produced. The lines isolated from these collections were named W. Va. A, W. Va. B, W. Va. C, respectively. All three lines showed a pronounced tendency to mutate, but mutations were especially numerous in line A. Nine mutants appeared within a short time and these were given numbers, thus: W. Va. A1, W. Va. A2, and so on to W. Va. A9. W. Va. A8 seemed a particularly promising line on which to make observations, as it soon produced eight distinct mutants. These in turn were numbered as follows: W. Va. A8-1 and so on to W. Va. A8-8. W. Va. A8-5, for example, indicates the fifth mutant from A8, which in turn is the eighth mutant from the original culture, W. Va. A. When the identity of a line is perfectly clear, as in tables and discussions of a series of mutants from one line, the locality designation sometimes is omitted for brevity. Thus, when it is clear that W. Va. A8-5 is meant, it is referred to simply as A8-5. When a number precedes the symbol for a given line, it shows how many times that line had been transferred in culture. For example, 10 W. Va. A8-2 would mean that W. Va. A8-2 had been transferred 10 successive times, and therefore had been in culture for a long period. This number is omitted except in certain cases in which it seems desirable to indicate the number of transfers that had been made.

Many different kinds of nutrient media were used during the course of the work. For stock cultures ordinary 1 per cent potato-dextrose agar generally was used. "Difco" agars were used for more careful work. The organism grows well on ordinary potato-dextrose agar, on potato-dextrose agar plus half strength Shive's solution, on potato-dextrose-maltose agar, and on several other media. While several different media were used, some of which cannot be standardized accurately, the media on which smut lines were grown for comparison always were made up in one batch and equal amounts were poured into each flask to be inoculated.

Stock cultures were grown in test tubes but other cultures were grown in Erlenmeyer flasks of about 250 cc. capacity, where differences in cultural characters were readily observed and mutants could be seen to best advantage.

HOW MUTANTS ARISE

Mutating colonies are clearly shown in Plate I. It will be noted that most of the mutants appear as wedge- or fan-shaped sectors in the colony; but they may appear also as irregular patches at various places on the surface of the colony, as described by Brown for Fusarium (8). These patches can be seen clearly in Plate I, B. A large percentage of the sectors are likely to develop near the edge of the parent colony, while the patches are most likely to appear nearer the center. Sometimes the margin of a colony may be almost entirely occupied by sectors of different sizes, and, in a few cases observed, the surface of a colony was covered almost completely with "patch mutants." The sectors vary greatly in shape, size, surface characters, consistency, sharpness of outline, and color, as will be noted from Plate I and Figure 3. By far the largest number of mutants observed by the writers appeared as rather sharply-defined sectors, and relatively few as patches.

Clearly defined sectors not infrequently appear within sectors. For example, in a colony of W. Va. A8-4-3 there were 6 distinct sectors near the margin, and a number of patches near the center of the colony. The colony itself was dirty yellow in color and the surface was coarsely reticulated, almost morel-like in appearance. One of the sectors was large, fan-shaped, smooth, and pale yellow; three of them were small, wedge-shaped, smooth, and bright yellow; the fifth was irregularly rectangular, smooth, except for tangential striae, and fuliginous in color. Within the last sector, and extending to the margin, there was a sharply-defined, black, wedge-shaped sector. The patches near the center were dull black.

It is evident that there would be no difficulty in detecting sectors like those shown in Plate I. But it is more difficult to see the patch mutants, especially when they are small and poorly developed. Under such circumstances it is often extremely difficult to make transfers from them, particularly if they are tough or viscous. One cannot always be sure of recovering even the parental form, as it seems certain that there may be many mutant primordia that are not observable at all. For this reason the writers sometimes restricted their efforts largely to the isolation of lines from the better-defined sectors in colonies that appeared relatively homogeneous except for the presence of the sectors, altho an attempt was made to take the mutants as they came.

Nevertheless, many probably were neglected, but there were several thousands more than could have been studied in any case, so the neglect did not seem serious.

FREQUENCY OF MUTATION

The 200 monosporidial lines isolated were distinctly and consistently different from each other in cultural characters, and, in our opinion, may properly be considered physiologic forms, altho they usually are referred to as lines in this paper. *U. zeae* evidently comprises quite as many distinct lines as does corn. And this is not surprising when one observes how readily some lines of the fungus mutate.

Most of the monosporidial lines studied have matured to a greater or less extent; altho some mutated more frequently than others. The 200 lines have given rise to thousands of mutants during a period of two years. Stability is the exception to the rule—even those lines that appear to be stable for a long time may suddenly mutate abundantly. This was true of Canada A and Texas A, which had been grown in culture about four years without mutating. Suddenly they

TABLE I

NUMBER OF MUTANTS PRODUCED BY MINN. A AND TWENTY OF ITS MUTANT LINES WHEN GROWN AT ROOM TEMPERATURE ON TWO DIFFERENT KINDS OF AGAR MEDIA, IN TRIPLICATE FLASKS OF EACH

Lines	Medium and number of mutants*		
	Potato dextrose + 1 per cent malt	Potato dextrose + 1 per cent malt + 2 per cent sucrose	Totals
Minn. A	6	9	15
A1	0	2	2
A1-1	0	0	0
A2	8	4	12
A3	8	7	15
A3-1	5	7	12
A4	8	0	8
A4-2	5†	5	10
A4-3	9†	6	15
A5	5	7	12
A5-1	8	6	14
A6	2	3	5
A7	0	0	0
A8	0	0	0
A9	0	1	1
A10	0	0	0
A11	0	0	0
A11-1	4†	6	10
A12	8	1	9
A13	..	0	0
A14	..	17	17
	76	81	157

* The potato-dextrose agar was 4 per cent "Difco"; the malt was Merck's powdered malt extract.

† Duplicate flasks.

began to mutate and are continuing to do so. Mutants may in turn mutate, also in varying degrees. (See Fig. 3.)

The differences in the tendency of various mutant lines to mutate are shown in Tables I, II, and III.

Of the 21 lines listed in Table I, all but 6 mutated, 17 being the largest number of mutants produced by any one line in the 6 flasks. In all, there were 123 flasks, one colony in each, and 157 mutants appeared in them. Of these, 69 were distinct, the others apparently being duplicates.

Table II shows clearly the differences in the tendency of different lines to mutate. In 6 colonies of W. Va. A8-4-3 there were 38 distinct mutants, an average of more than 6 in each colony, while there were only 2 in 5 colonies of A8-4, the immediate parent. There also were 38 mutants in 6 colonies of A8-5-3. On the other hand, there were none in 4 flasks each of A8-4-2 and A8-4-5. In a total of 64 colonies in this experiment, 134 mutants appeared, an average of more than 2 a colony, and 2 lines of the 12 contributed more than half of this number. But perhaps the most conspicuous example of differences in lines with respect to mutation is the fact that, of the 162 distinct mutants derived from W. Va. A8, one line, A8-5, gave rise to 112 in 5 cultural generations, while A8-7, A8-8, A8-9, and A8-10 gave rise to none at all.

TABLE II

NUMBER OF MUTANTS THAT APPEARED IN CERTAIN MUTANT LINES OF *Ustilago Zeae* DERIVED FROM W. VA. A8, GROWN ON THREE DIFFERENT NUTRIENT AGAR MEDIA IN DUPLICATE FLASKS FOR EACH MEDIUM

Lines	Medium and number of mutants			
	Potato dextrose	Potato dextrose plus half strength Shives' solution	Litmus lactose	Totals
W.Va A8-4	2	0	0*	2
A8-4-1	4	0	4*	8
A8-4-2	0	0	..†	0
A8-4-3	12	25	1	38
A8-4-4	2	..	1*	3
A8-4-5	0	0	..†	0
A8-5	1	9	2*	12
A8-5-1	5	2	3	10
A8-5-2	2	0	2	4
A8-5-3	9	20	9	38
A8-5-4	2	1	2	5
A8-5-5	5	2	7	14
	44	59	31	134

* One flask only.

† Both flasks discarded.

Two sporidia were isolated from a single promycelium and observations made to determine the relative frequency of mutation in the two resulting monosporidial lines, Minn. A and Minn. D, grown on 6 different culture media. The results are given in Table III. It will be noted that Minn. A produced 33 mutants, some on all media except one. Only 5 indistinct sectors appeared in colonies of Minn. D, on the other hand. This indicates that there probably was a segregation of factors that either directly or indirectly govern mutability. It had been found previously that the two lines were of opposite sex;[4] therefore segregation of sex factors certainly had taken place.

TABLE III

NUMBER OF MUTANTS THAT APPEARED IN CULTURES OF TWO MONOSPORIDIAL LINES OF *Ustilago Zeae* DERIVED FROM SPORIDIA OBTAINED FROM THE SAME PROMYCELIUM

Medium*	No. flasks	Lines of *U. zeae* and number of mutants	
		Minn. A	Minn. D
4.5% Potato dextrose	2	4	0
3.5% do	2	6	0
2 % do plus 2% cornmeal	3	8	0
4 % do plus 0.5% peptone	3	6	5†
4 % do plus 2% sucrose	3	8	0
Half strength Shive's solution plus 1.2% agar plus 3% dextrose	3	1	0
Half strength Shive's solution plus 1.2% agar plus 3% dextrose plus 3% lactose	3	0	0
Total	19	33	5

* "Difco" potato dextrose and cornmeal agars were used.
† Sectors in Minn. D not sharp.

It seems evident from Tables I, II, and III not only that there are wide differences in the mutability of monosporidial lines but that mutation occurs with surprising frequency in some. To study all of the thousands of mutants that appeared was obviously impossible without enlisting the services of a small army of investigators. It was decided, therefore, to select two lines for more intensive study.

Detailed observations were made on two monosporidial lines of opposite sex, W. Va. A8 and Minn. A. The latter produced 70 distinct mutants and the former, 162 by the fall of 1928. Since that time many more have appeared, but they are not recorded here. Figures 1 and 2 represent graphically the sequence of origin of the first 162 and 70 mutants of these two lines, respectively.

As the largest number of mutants came from W. Va. A8, a brief history of this line is given. The original chlamydospore material was obtained from Dr. R. J. Garber, of the University of West Virginia. In the early spring of 1927 dilution plates were poured. On May 3 transfers were made to three flasks of potato-dextrose agar, and nine sectors appeared in the three colonies. These sectors were considered probable mutants, despite the fact that monosporidial isolations had not yet been made. It is possible that they were segregates, but this seems improbable because no colonies resembling them had appeared in the

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[4] Dr. W. F. Hanna made the original sex determinations.

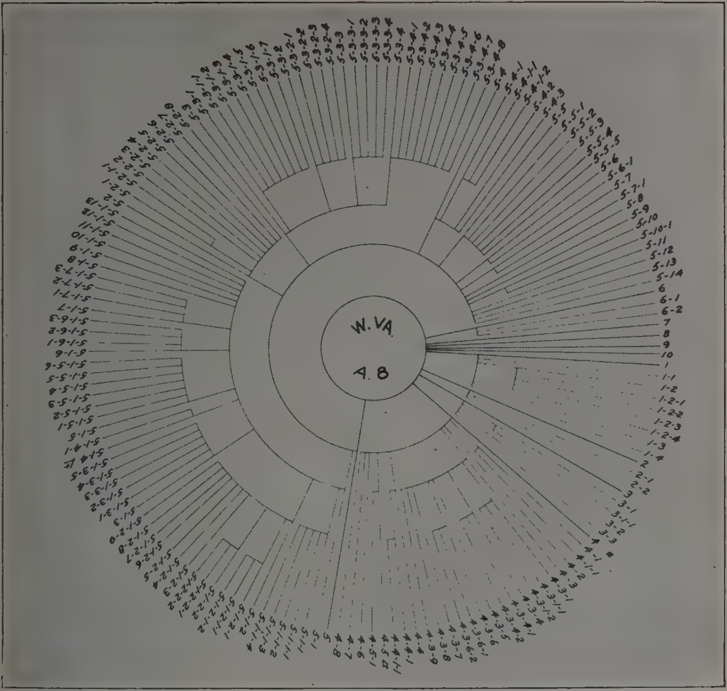

Fig. 1. Diagram showing the origin of 162 mutants from one monosporidial line of *U. zeae,* W. Va. A8.

original plates. Furthermore, the sectors appeared near the periphery of colonies about 35 mm. in diameter, and it seems likely that the colonies would have appeared heterogeneous while still fairly young, had several segregates been growing together. In fact, flasks were inoculated at various times with two or more lines of distinctly different appearance, and, altho it could be seen clearly that the colonies comprised several lines, these lines did not arrange themselves into sectors. It seems probable, therefore, that A8 was a mutant, altho it is not certain. The parent colony was light buff to tan in color, with a pinkish tinge near the center. The surface was slightly coral-like near the center and dull, china-like elsewhere. It was beautifully marked with very fine concentric lines. The sector was decidedly olivaceous, smooth except for fine concentric lines like those on the parent colony, and bordered with a feathery to powdery fringe. A transfer was made from this sector and several successive transfers were made subsequently. In January, 1928, a single sporidium was isolated, and the resulting line was then used for the study of mutation.

The monosporidial line of W. Va. A8 began to mutate as soon as colonies resulting from transfers became available for study. By

March 8, mutants A8-1, A8-2, etc., had appeared. They were compared under uniform conditions and were decidedly different in appearance on several kinds of culture media. All of these mutants in turn mutated except A8-7, A8-8, A8-9, and A8-10. By the fall of 1928 a total of 220 mutants had been isolated, and it was decided to discontinue selecting and culturing new ones which were appearing, as the process seemed to be going on ad infinitum.

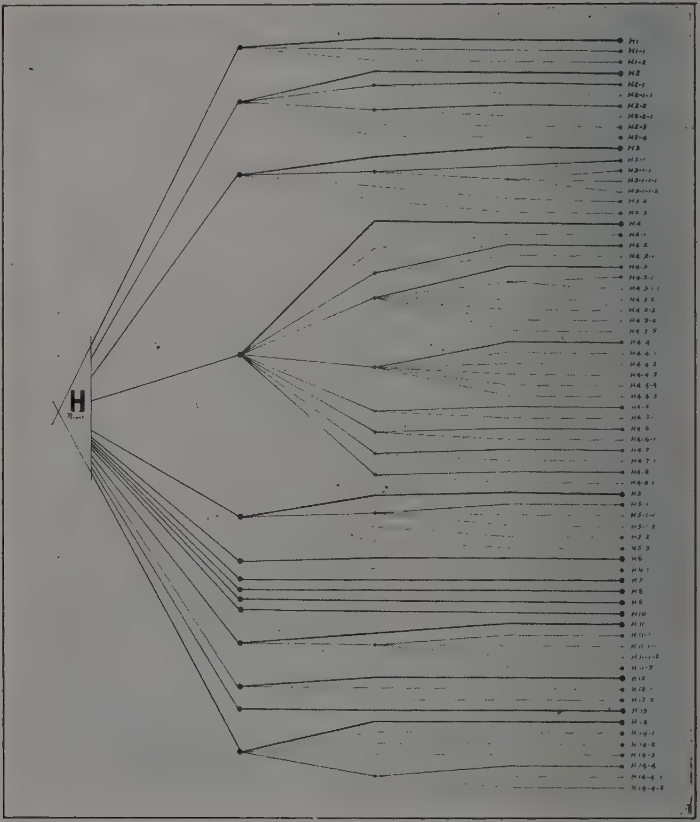

Fig. 2. Graphic representation of the origin of 70 mutants from one monosporidial line of *U. zeae*, Minn. A (designated in diagram by H).

The 220 mutants were transferred on November 24 to agar slants in order to obtain cultures of the same age for inoculating flasks for comparison of cultural characters. On December 1, each mutant line was transferred to triplicate 250 cc. Erlenmeyer flasks, each containing 35 cc. of nutrient agar made up of potato extract, 1.8 per cent agar, 1 per cent dextrose, 1 per cent sucrose, and 1 per cent Trommer's malt extract. It is realized, of course, that the composition of a medium made up with potato extract as a base might vary greatly when made up at different times, but the objection of variability would not apply to a single comparative test such as was made in this case. The agar was made up in one batch, 35 cc. poured into each flask, and all of the 660 flasks sterilized at the same time in a large steam-pressure sterilizer.

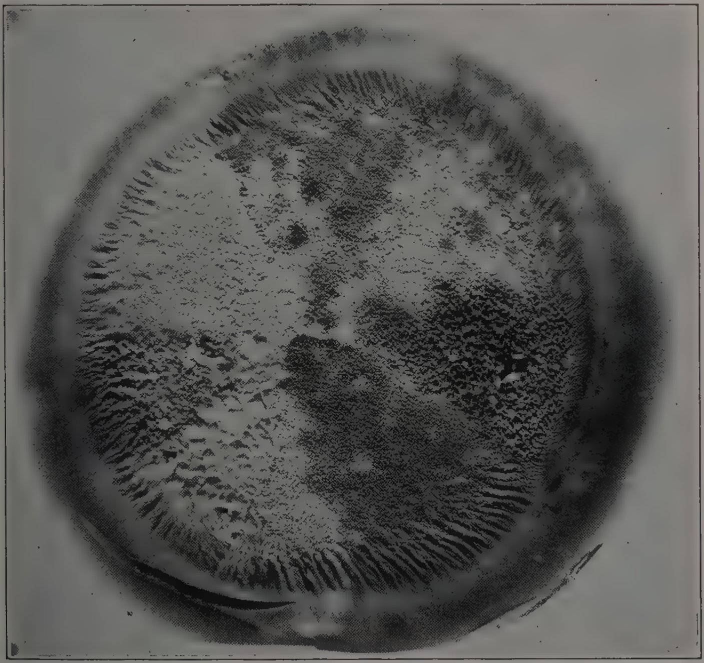

Fig. 3. Minn. A3-1-1-2-1-1, which originated through six successive mutations, still producing mutants.

At the end of four weeks notes were taken on the cultures. It appeared that 38 lines were duplicates, 4 triplicates, and 4 quadruplicates, leaving 162 that were decidedly distinct from the parent and each other, with the possible exception of one that resembled the parent somewhat and one that apparently had lost the ability to grow. Of the 162 distinct lines, 112 were derivatives of A8-5, showing again the differential tendency of lines to mutate. The 58 discarded lines may have been different in characters other than gross cultural characters, or they might have been distinct in appearance had they been grown on other culture media, so it is unsafe to conclude that they actually were identical with some of the other lines. However, the amount of work required to settle the question seemed disproportionate to the probable value of the results, and the task was not undertaken. It is known, of course, that apparently identical mutants may arise independently and that there may be mutations to the parental type; consequently it would not be surprising to find almost identical lines among a large number of mutants.

Minn. A also mutated very frequently. It is noteworthy that the first 70 mutants isolated in succession from this line were distinctly different from the parent and from each other.

Some of the mutants were relatively stable in culture, while others were very unstable. (See Tables I, II, and III.) No mutations have been observed in Minn. A9 and Minn. A10, for example, altho they have been grown for 21 months on many different kinds of media. It is not unlikely, however, that they may begin to mutate at any time. Minn. A13 had been grown in culture for more than a year and had been transferred at least a dozen times, without any indication of mutation until the winter of 1928-29, when it suddenly began to mutate and has continued to do so through several successive cultural generations.

There were similar differences in the mutability of mutant lines of W. Va. A8. For example, A8-1 gave rise directly to four mutants which in turn gave rise to 13, many of which again mutated. In one case 15 mutants appeared in a single colony of W. Va. A8-4-3. Of the 162 distinct lines, 112 were derivatives of A8-5. On the other hand, A8-7, A8-8, A8-9, and A8-10 have produced no mutants whatever.

MUTANT CHARACTERS

Mutants may differ from their parents in several respects. They may differ decidedly in cultural characters, including rate of growth, direction of growth, general appearance of the colonies, and pigmentation. There is evidence that morphological changes also may occur. Parent colonies may consist of sporidia, and the mutants almost entirely of mycelium or vice versa. The mutants may differ from their parents also in general physiologic characters, in their tendency to mutate, in sexual characters, and in pathogenicity.

General Cultural Characters

General statement.—Mutants may differ from their parents in one or more of the following general cultural characters: rate of growth, type of growth and consistency of the colony, surface characters, and color.

An idea of the differences in general cultural characters of mutants can be gained from Tables IV and V, in which are listed some of the characteristics of mutants grown on potato-dextrose-maltose agar and on 2 per cent potato-dextrose agar plus a trace of methyl orange. It is perfectly clear from Tables IV and V and from Plates II, III, and IV that there may be very wide differences in the general appearance of colonies of mutants which originated from the same monosporidial line. Numerous comparisons similar to those listed were made with these same mutants and with many others. As a matter of fact, the principal cultural characters of the 70 mutants in the Minn. A series and the 162 derived from W. Va. A8 have been carefully recorded, but it seems scarcely worth while to give them all in detail.

The following notes taken on colonies in triplicate flasks of potato-dextrose agar may give an idea of the difference in appearance of mutants from the same parent.

W. Va. A8-4: Colonies 40 mm. in diameter, roughly convoluted, orange-buff in color; mid-size radial ridges, about 5 mm. long, extending in clockwise direction near the edge of the colony; delicate opaque margin, about 6 mm. wide

W. Va. A8-4-1: Colonies 43 mm. in diameter, less convoluted than those of A8-4, with a tendency to form fine ridges radiating from the center and ending in radial ridges as above, but extending in a decidedly counter-clockwise direction; margin about as in A8-4; color approximately the same as in A8-4.

W. Va. A8-4-2: Colonies 43 mm. in diameter; surafce convoluted into low folds; radial ridges somewhat as in previous two lines, and extending in slightly clockwise direction; central area of colony grayish-buff in color, and margin pearl-gray.

W. Va., A8-4-3: Colonies 50 mm. in diameter; grayish to mauve in color; surface coral-like; colony very thin; margin pale ivory in color.

W. Va. A8-4-4: Colonies 40 mm. in diameter; coarsely convoluted as in A8-4; center orange-brown in color and remainder deep-buff orange; radial ridges similar to those of A8-4 but much finer and straight or very slightly clockwise.

W. Va. A8-4-5: Colonies 40 mm. in diameter, coarsely convoluted; very coarse and distinct radial convolutions and deep marginal ridges; colony deep orange throughout except on the marginal ridges which are somewhat paler in color than the rest of the colony.

The salient cultural characters of 8 mutant lines of W. Va. A8 are given in Table IV and are shown in Plate IV. The different lines had been grown in culture from 10 to 14 months, on many kinds of media, and under various environmental conditions. Late in July, 1929, all were transferred to flasks of potato-dextrose-malt agar for temperature relation studies. Notes on cultural characters of duplicate flasks incubated at 26° C. were taken on September 1, 1929. The duplicate colonies of the same line were as nearly identical in appearance as could have been expected. But the appearance of those of different lines differed so greatly that several people, who scarcely knew the meaning of the word fungus, could readily sort the lines from a random arrangement into the proper groups.

Descriptions and uncolored photographs are quite inadequate to convey a clear idea of the remarkably nice differences in appearance of cultures of different lines. To paint a faithful word picture of the colonies is virtually impossible; and photographs do not show the sometimes decided and sometimes slight but extraordinarily beautiful differences in color. In descriptions of cultural characters differences may appear to have been drawn too finely to be real, but the astonishing fact is that they actually are so very real and so entirely characteristic of certain lines of the fungus.

It will be seen from Table IV and Plate IV that cultures of the lines listed differed from each other considerably in size of colony, color, luster, surface, and margin. In fact, so different are the cultural characters of different mutant lines grown under uniform conditions that many lines would be suspected of belonging to different species.

Type of growth.—Some lines may produce mycelium and others sporidia almost exclusively. A mycelial colony may produce aerial sporidia, and hyphae may be present to a certain extent in sporidial colonies, depending on the culture medium and other conditions. In other cases, however, the colonies consist almost exclusively of mycelium or sporidia. For example, W. Va. B was wholly mycelial whereas its mutant, W. Va. B5, was wholly sporidial. Sporidial colonies often produce mycelial mutants which usually grow more rapidly than the sporidial parent and can be more easily selected and propagated. As a matter of fact, it seems likely that the difficulty of maintaining the sporidial type in stock cultures is due largely to the fact that mycelial mutants develop abundantly, grow rapidly, and therefore are likely to be transferred instead of the sporidial parent. Some sporidial lines, however, can be propagated and maintained for a long time in culture if sufficient care is exercised in making transfers. Texas A, a sporidial type, for example, has been kept in culture for at least four years, and several other lines have been maintained for more than a year, but they have given rise repeatedly to mycelial mutants. Both mycelial and sporidial lines usually give rise to mycelial mutants, but not necessarily so. As indicated, some mycelial lines have produced sporidial mutants also.

In colonies of mycelial lines the hyphae may be coarsely tufted, finely tufted, or even silky. There appear to be all gradations in the size of hyphae as well as in the manner in which they are aggregated into mats of woolly, felty, cottony, or silky appearance and texture.

Consistency of colonies.—As would be expected from the fact that there is so great a range in the type of growth, there is the greatest range in the texture and consistency also, as they depend to a considerable extent on the type of growth.

The consistency of colonies on agar media may be slimy, butyrous, viscid, brittle, powdery, membranous, or coriaceous. And sectors of any one of these consistencies may arise in colonies of any other type

TABLE IV

Cultural Characters of Eight Lines of W. Va. A8 Derivatives Growing in Duplicate Flasks of Potato-Dextrose Agar

Line	Diam. in mm.	Color	Elevation	Luster	Surface and topography	Edge
A8-5-3-3-2	50	White; faint purple brown near center	Convex	Cretaceous	Verrucose	Slightly fimbriate
A8-5-4	43	Orange brown; margin faint orange, covered with white powder	Broadly umbonate	Dull in center; marginal band powdery	Somewhat contoured; marginal band with small radiating ridges	Erose to lobate
A8-3-1	56	Gray drab on central knob; surrounded successively by olive drab, gray drab, and dirty yellowish-white zones	Convex-umbonate	Dull to cretaceous	Central area rugulose; surrounded by coarsely rugose zone, and broad marginal zone almost flat; radial folds extending 1 centimeter from central area but not reaching margin	Fimbriate
A8-1-1	18	Pinkish buff	Pulvinate	Dull waxy	Rugose to rugulose	Finely lobate to auriculate
A8-5-7-1	50	Gray brown in central zone; surrounded by narrow dark brown band, then buff brown and margin brownish gray	Flat	Dull	Zonate; smooth, finely felty	Somewhat plumose
A8-5-2-1	40	Whitish brown to smoke gray	Raised to convex	Cretaceous	Rugose; irregular radial furrows near margin and tendency for folds to crack irregularly	Somewhat lobate
A8-5-5	55	Orange buff	Convex	Dull	Contoured; regular radial furrows in marginal zone	Entire
A8-5-3-2-5	45	Purple brown, with white powder in central and marginal zones	Convex	Dull to cretaceous	Coarsely verrucose; closely branched radial ridges in marginal zone	Undulate

of consistency. For example, the colonies of a monosporidial line of Italy C were dark purple in color and felt-like or coriaceous in consistency on potato-dextrose agar. Two large sectors appeared in one colony, one of which was cinnamon brown with a tinge of purple in color and rather brittle in consistency, while the other, a very rapid grower, was Jews-ear fungus-like in appearance and butyrous in consistency. On the other hand, the consistency of colonies of W. Va. A8-3 was butyrous, but that of A8-3-1, which appeared as a large, fan-shaped sector, was decidedly coriaceous. Again, the consistency of A8-4 was brittle, while that of 4 sectors ranged from membranous to coriaceous.

There are all degrees of viscosity. Transfers are easily made from some colonies, especially the butyrous type. Inoculum can be obtained by dipping a loop of small gage wire into the colony. Some colonies are so viscid, however, that it is only with great difficulty that inoculum can be obtained, even with a stiff wire. Colonies may be only slightly viscous while others may be doughy or even gummy in consistency. Still others may be so brittle or powdery that it is necessary to moisten the inoculating needle before sufficient inoculum will adhere to it. Some colonies are so membranous that it is necessary to cut out small squares to avoid lifting the entire colony with the inoculating needle. It was necessary to make a small, sharp-edged spatula to cut small pieces of inoculum out of some of the colonies that were tough, felty, or almost leathery. Colonies also may be cottony, silky, or fluffy. And all of these types can be found in mutants derived from one or two monosporidial lines.

Direction of growth.—The direction of growth often is subject to mutation. The mycelium of some mutants has a tendency to grow in a clockwise direction, that of others in a counter-clockwise direction and that of still others in a strictly radial direction. Mutants characterized by any one of the three directions of growth may be obtained from the same line, sometimes from the same colony. (See Table V.) The difference in direction of growth is illustrated in a series of mutants which arose in triplicate flasks of W. Va. A8-4. The direction of growth is indicated in the following summary:

A8-4: Mid-size ridges about 5 mm. long near the margin of colony; direction decidedly clockwise.

A8-4-1: Fine radial ridges extending to within about 10 mm. of edge, then an area of ridges as above, but direction decidedly counter-clockwise.

A8-4-2: Fine radial ridges; direction slightly clockwise.

A8-4-3: No ridges.

A8-4-4: Ridges as in A8-4, but finer and straight or very slightly clockwise.

A8-4-5: Very large ridges near margin; direction straight.

Mutation in direction of growth is illustrated also by Italy A. The parent colonies were lavender to purple in color, and smooth except for rather fine radial ridges extending from the center about half way to the margin. There was no appreciable turning of the ridges in either direction. A1 and A2 arose as sectors. A1 was quite similar to the parent except that the radial ridges or folds were much larger, extended farther toward the margin, and turned in a decidedly clockwise direction. In A2 the color was grayish buff and the whole surface was covered with coarse ridges that united to form a beautiful reticulum, the colony resembling the surface of a small morel.

Microscopic examination was made of A and A1 and it was found that the hyphae of A grew straight, while those of A1 curled, explaining the clockwise growth of the ridges.

Direction of growth is somewhat variable but there is a general tendency for it to be fairly constant under one set of conditions, altho not necessarily so under different conditions. The counter-clockwise direction of growth is illustrated in Plate III.

Size of colonies.—Mutants may grow more rapidly or more slowly than their parents. Many observations and tests were made to ascertain the difference in rapidity and extent of growth of mutants as compared with that of their parents and other mutants. Observations usually were made in triplicate flasks for each medium, altho sometimes duplicates were used. The diameter of the colonies was measured in two directions at right angles to each other, and when the colony was not circular the results were averaged. Tables V and VI give the

TABLE V

SIZE, TYPE OF GROWTH, DIRECTION OF GROWTH, AND NUMBER OF SECTORS IN COLONIES OF 16 MUTANT DERIVATIVES FROM MINN. A GROWN ON 2 PER CENT POTATO-DEXTROSE AGAR PLUS A TRACE OF METHYL ORANGE

Mutants	Diameter of colony in mm.	Direction of growth*	Type of growth	Aerial† mycelium	Number of sectors
Minn. A2-2-1	33	cc+	Mycelial	0	6
A2-4	31	c±	do	++	10
A3-2	32	cc±	do	0	1
A3-1-2	36	cc++	do	+++	0
A4-2-1	30	0	do	0	1
A4-3-5	23	0	do	0	7
A4-4-3	28	cc++	do	0	9
A4-4-4	31	0	Sporidial	0	0
A4-6-1	29	cc+++	Mycelial	++	2
A5-2	38	0	Sporidial	0	0
A12-1	38	cc+	Mycelial	0	3
A13	47	0	Sporidial	0	0
A14	28	0	Semi-sporidial	0	25
A14-2	38	0	do	±	13
A14 3	28	0	do	0	19
A14-4-2	32	c+	Mycelial	++++	11
					107

* cc = counter-clockwise growth; c = clockwise growth; + = degree of turning.

† 0 = no aerial mycelium; + = aerial mycelium present, the amount indicated by number of + signs; ± = slight amount.

diameters, in millimeters, of colonies of several mutants and their parents on two different media. It is evident that there were considerable differences in the rate of growth and the size of the colonies of different mutants. For example, on malt-sucrose agar the diameter of the parent, Minn. A, at the end of 11 days was 25 mm. while that of A4-6 and A11-1 was 19 mm. and those of A11, A13, and A14 were 49, 45, and 33 mm., respectively. It is obvious that some mutants grow much more slowly than their parents while others grow far more rapidly. (See Table VI.)

TABLE VI

Rate of Growth of Minn. A and Some of Its Mutants As Measured by the Diameters of Colonies on Two Different Agar Media

Lines	Medium and diameters of colonies in mm.*	
	Potato dextrose + 0.5 per cent glycerine + trace of gentian violet	Potato dextrose + 1 per cent malt
Minn. A	15	25
A3-1	18	24
A4-2	10	24
A4-3	12	21
A4-6	15	19
A4-7	18	20
A8	18	21
A9	11	21
A10	8	22
A11	18	49
A11-1	17	19
A12	21	21
A13	..	45
A14	..	33

* The potato-dextrose agar was 4 per cent Difco; diameter of colonies listed in first column is the average of 2 colonies, 33 days old, and in the second column of 3 colonies, 11 days old.

There were remarkably consistent differences in the size of the colonies of a series of mutants from W. Va. A8-4, grown for purposes of comparison on potato-dextrose agar, potato-dextrose agar plus one-half strength Shive's solution, and litmus-lactose agar. The parent produced colonies with diameters of 45, 45, and 55 mm. on potato-dextrose agar, Shive's agar, and litmus-lactose agar, respectively, whereas A8-4-4 produced colonies with diameters of 50, 50, and 60 mm., respectively. In this particular case the diameter of the colonies of the mutant was 5 mm. greater than that of the parent on all three media. In other cases in this series the size of the colonies of certain mutants was approximately the same as that of the parent. These differences in rate of growth sometimes are observable only on certain media. For example, 13 mutants arose from W. Va. A8-5-1. One of these, W. Va. A8-5-1-5, produced two large mutants which looked almost identical, and were labeled A and B tentatively until it could be ascertained whether they actually were identical. Both were transferred on the same day to two flasks each of potato-dextrose agar, potato-dextrose plus half-strength Shive's solution agar, and litmus-lactose agar. On potato-dextrose agar the two were so nearly alike that they might easily have been considered identical. On litmus-lactose agar they were fairly distinct in appearance but not in size. On the Shive's solution agar, however, the colonies were quite distinct, both in general appearance and in size. The colonies of A were 40 mm. in diameter, whereas those of B were 50 mm. This shows that it is necessary to consider the media on which the cultures are grown in determining rate of growth and size of colonies. A mutant may grow much more rapidly than its parent or other mutants on one medium, but the result may be the exact opposite on another.

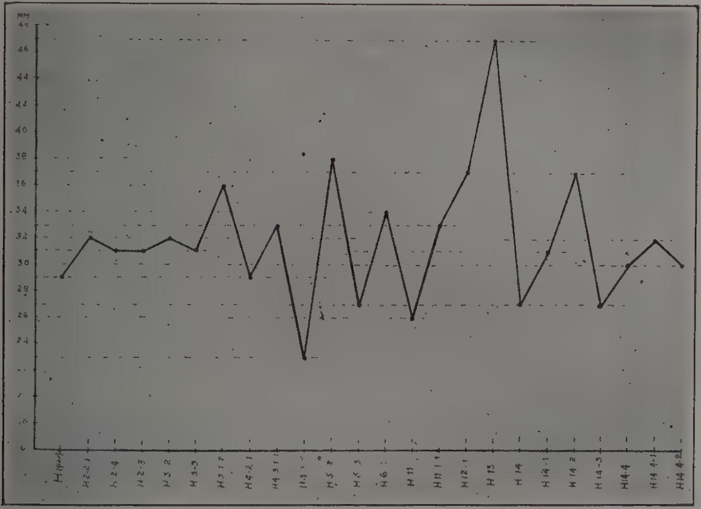

Fig. 4. Differences in the diameters of colonies of 23 mutants and their parent, Minn. A (designated in diagram by H), when grown on potato-dextrose-sucrose-malt agar.

The most extensive series of measurements were made on derivatives of W. Va. A8. It will be recalled that 220 mutants were obtained from a monosporidial culture of this line. Of these, 162 were distinct. When final observations were made on the 220 lines, the diameters of the colonies were measured. There were three flasks of each line, but only the average is given in Table VII. In most cases there was very little difference in the size of the three colonies of the same line, usually not more than 3 or 4 mm., altho in some cases there was greater variation. In general there was so little variability within the lines that the results seemed indicative of the genotypic tendency of the different lines to produce colonies of a certain size. The class intervals, as will be seen from Table VII, are 8 mm. This seems sufficiently large because the fact had been determined by repeated observations that colonies of the same line seldom vary so much under uniform conditions.

TABLE VII

SIZE CLASSES OF COLONIES OF 180 MUTANTS DERIVED FROM W. VA. A8, GROWN ON THE SAME MEDIUM AND UNDER SAME CONDITIONS IN TRIPLICATE ERLENMEYER FLASKS OF UNIFORM SIZE

Class intervals in mm.	Number and percentage in classes	
	No.	Per cent
30-37	23	13
38-45*	82	45
46-53	61	34
54-61	14	8
Total	180	

* Parent falls into this class.

Measurements are available for 180 of the lines. The line producing the smallest colonies was A8-5-12. These measured 28, 31, and 30 mm., respectively, an average of about 30 mm. That producing the largest was A8-5-1-2a-3, with colonies 61, 58, and 61 mm., an average of 60. The extreme range in size between the colonies of different mutants was 30 mm., the largest being twice the size of the smallest.

One usually thinks of mutants as having lost certain factors. However, some of this series have acquired growth factors or have lost factors that inhibit growth. This is evident when one considers that of the 180 lines compared, 82 produced colonies of the same size class as those of the parent, 23 produced smaller colonies, and 75 produced colonies larger than those of the parent, or 45, 13, and 42 per cent, respectively. It is possible that this does not represent exactly the true state of affairs. The more rapidly growing sectors are most conspicuous in a colony, and possibly a larger proportion of them were selected than of the smaller ones. Furthermore, in some lines of smut there is a tendency for the production of very small patch mutants, many of which probably never are isolated. Altho an attempt was made to select all that developed, regardless of size, it is likely that many mutant primordia are formed, but never become large enough to be observed clearly.

Many mutants derived from Minn. A and from W. Va. A8 have been grown repeatedly in different liquid media. There were decided differences in rate and amount of growth, as indicated by the mats sometimes formed on the surface, by the amount of flocculent material in the medium, and by the amount of sediment on the bottom of the flask. The differences in the character and amount of growth in the various flasks were quite as sharp and great as similar differences in the growth of many species of bacteria in liquid media.

Elevation of colonies.—Not only are mutants characterized, to some extent, by the amount of radial growth of colonies, but also by their elevation. Colonies may be effuse, flat, raised, convex, pulvinate, capitate, umbonate, umbilicate, or combinations of several. There are types also that scarcely fall into any class. Thus in W. Va. A8-5-2-1 there is a tendency for part of the colony to separate from the remainder along a horizontal plane and to assume a somewhat irregular cupulate form, especially at low temperatures. This habit is peculiar to this particular line. The effuse and umbilicate types probably are the rarest, altho effuse colonies are common on poor media. It can be seen from Table IV that there are several types of elevation, even in a more or less random sample such as the lines listed in the table comprise.

Sometimes a particular type of elevation is so peculiar to colonies of a certain line that it alone almost suffices for identification. W. Va. A8-5-4 can be distinguished from many similar lines by the broadly umbonate character of its colonies, in which there is a broad, thick, central mound, often 25 mm. in diameter, surrounded by a flat zone of different color. (See Plate IV.)

Color of colonies.—There may be a wide range of color mutations in a monosporidial line. Albino mutants arise frequently in colonies of various colors; the color of mutants often but not always is lighter than that of the parents. There may be an intensification of color, or even a complete change, as well as a loss. (See Plate I.) Plate I, B shows one pure white sector, two dark ones with white margins, and several that are as dark as, or darker than, the parent. In Plate I, A are shown several sectors that are much darker than the parent.

Sectors or patches of several different colors often appear in duplicate colonies or even in a single one. In fact, almost any combination may occur. For instance, there appeared in duplicate pinkish colonies of W. Va. A8-4 sectors with the following colors: white, ivory, yellow, olivaceous, and black. In one pinkish colony of W. Va. A8-5 growing on potato-detrose plus Shive's solution agar there were 6 sectors colored as follows: white, cream-colored with a tinge of pink, grayish purple, olive, London smoke, and black. Minn. A14 was wood-brown and gave rise to sectors with the following colors: white, fawn, auburn, and pale vinaceous drab, the latter subsequently producing one of army-brown color.

The following colors were recorded for Minn. A and 6 of its mutants: Minn. A, pallid mouse gray; Minn. A1, seal brown; Minn. A2, vinaceous buff; Minn. A3-1-1-1, ecru drab; Minn. A10, blackish brown;

Minn. A11-1-2, white; Minn. A11-2, straw yellow. The following range of colors appeared among the 162 mutants from W. Va. A8; white, ivory, pearl gray, light buff, tan, light orange, deep orange, orange brown, and purple brown.

Color is not always uniform throughout a colony—there may be two or more color zones. This is well illustrated by W. Va. A8-5-7-1. (See Table IV and Plate IV.) The color may be masked somewhat by the production of aerial conidia that may give the surface a powdery or chalky appearance that may be so pronounced as almost to obscure the color underneath.

The color of colonies is, of course, subject to great variation under different environmental conditions. A culture, for example, may be cream-colored on one medium and almost black on another. Under similar conditions, however, color is fairly constant and quite characteristic of the mutant lines. This is well illustrated by the following observation. On September 10, 1928, one of the writers noted that colonies of W. Va. A8-5-4 were much darker orange brown on potato-dextrose agar than those of W. Va. A8-5-1. Soon thereafter the cultures of this series were given to another person for experiments on physiologic characters. The writer saw them again, quite by chance, on September 1, 1929, and again noticed the decidedly deeper color of A8-5-4. Upon looking at his original notes to see how the colors had been recorded a year previously, he found that they coincided almost exactly with his new observations, altho the cultures were on a slightly different medium.

The luster of colonies of different mutant lines may differ considerably, partly depending upon whether the colonies are sporidial or mycelial. Sporidial colonies may be either glistening or dull, while mycelial colonies naturally are dull, powdery, or cretaceous. Aerial conidia may be produced in either case. The result is likely to be a powdery appearance, thus modifying the color of the colony.

Surface characters of colonies.—It is clear from Plates II, III, and IV that the surface characters of colonies of different mutants may differ greatly. In the case of the mycelial type of growth the surface may be waxy, pubescent, cottony, felty, or finely or coarsely tufted. It may be smooth, or contoured, rugose, verrucose, bullate, or reticulate. In contoured colonies there again is considerable variation. In rugose colonies the folds may extend principally in one direction or in several. They may be simple or branched and anastamosing, giving all sorts of appearances from fine to coarse coral-like, sponge-like, or morel-like—some of which are very beautiful. Again, the size of the folds may vary. They may be large, small, or intermediate, and may be wide or narrow, and ridge-like rather than foldlike. There also are all degrees of fineness and coarseness of the verrucose condition in colonies with this type of topography.

The marginal characters of colonies vary greatly with the different lines. In some cases the margin is entire, in others undulate, lobate, erose, lacerate, fimbriate, or floccose. Very often there is a distinct marginal zone in which the consistency, surface characters, luster, and color are quite different from those of the body of the colony. There may be a white border on deeply colored colonies, or it may be darker in color than that of the remainder of the colony. Sometimes there is a border of fine, silky hairs, ranging in width from two or three millimeters to a centimeter or more. Again, the border may be characterized by the presence of radial ridges or furrows of various shapes and sizes, whereas the remainder of the colony may have a quite different topography.

The surface of colonies may be uniform throughout or characteristically zoned. The zones may differ in topography or color, or both. (See Plate IV.) As all 8 lines shown in Plate IV are mutant derivatives of W. Va. A8, it is evident that the factors for zonation are subject to mutation. W. Va. A8-5-7-1 has several distinct color zones, but the topography is uniform throughout the colony, while in A8-5-4 the two zones differ in both color and topography. The same is true of A8-3-1, A8-5-5, and A8-5-3-2-5. It is interesting to notice that A8-5-4 and A8-5-5 appeared as sectors in the same colony of A8-5. Both have radial ridges in the marginal band, altho there are differences in their characters, but the color of the band in A8-5-5 is only slightly lighter than that of the remainder of the colony, while in A8-5-4 it is always much lighter, often becoming pure white.

Physiologic Characters

General statement.—Mutations often, perhaps almost always, involve some change in physiologic characters that are not so obvious as changes in general cultural characters. It was observed a number of times in studying the influence of media on frequency of mutation that certain lines of *U. zeae* changed the color of litmus media more than others, and there seemed to be some differences in ability to absorb dyes. On media containing litmus it sometimes was possible to pick out certain mutants readily by the color change produced by them, indicating that they were producing a reaction different than their parents.

Some preliminary experiments were made in order to determine differences in alkali production. Seven mutant lines were grown on slightly acid potato-dextrose agar to which was added a trace of bromcresol-purple indicator. The production of alkali is indicated by a change in the color of the medium from yellowish to deep purple.

The results are summarized in Table VIII. It is evident that Minn. A3-1-2 produced alkali more rapidly and in larger amounts than A4-4-5 and A1-1. The differences were very striking during the first week or two of growth, but at the end of three weeks all of the mutants had produced a deep purple color. There was no obvious relation between the rate of growth and the rate of alkali production. For example, A3-1-2 grew slowly, but produced alkali rapidly, while A1-1 grew rapidly, but produced alkali slowly. The tests were repeated on potato-dextrose agar plus ½ per cent litmus solution, with similar results. (See Fig. 5.)

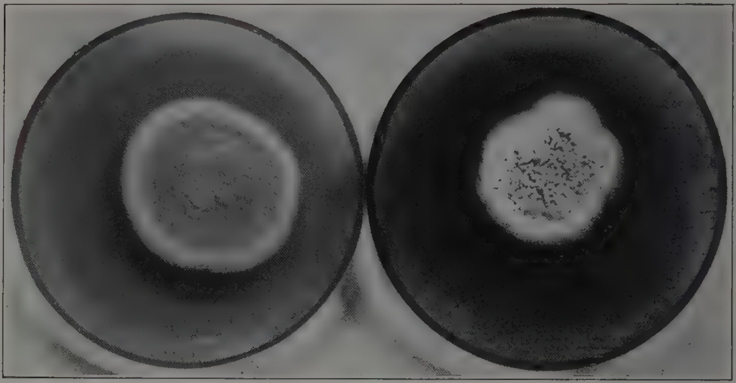

Fig. 5. Two mutants grown on potato-dextrose agar + brom cresol purple, showing differences in alkali production as indicated by intensity of color: *Left,* Minn. A1-1; *Right,* Minn. A3-1-2.

TABLE VIII

RATE OF GROWTH AND ALKALI PRODUCTION OF MINN. A AND EIGHT MUTANTS AS MEASURED BY DIAMETER OF THE COLONIES AND THE COLOR REACTION ON POTATO-DEXTROSE AGAR PLUS A TRACE OF BROM-CRESOL PURPLE

Lines	Degree of alkali production*			Diameter of colony in mm.
	14 days	18 days	22 days	18 days
Minn. A	+	++	+++	41
A1	+	++	+++	45
A1-1	o†	o†	++±	42
A3	o	o†	++±	38
A3-1-2	+++‡	+++	+++	36
A4	o	+	+++	36
A4-4-5	o	o†	++±	28
A10	±	+±	+++	38
A3-1-1-2-1-1-1-3	±	+±	+++	39

* o = none; + = alkali production, the degree being shown by number of signs; ± = slight.

† Purple under colony; no diffusion.

‡ Entire medium deep purple.

There also were marked differences in the ability of different lines to absorb indicators or dyes. For example, Minn. A4-4-5 absorbed brom-cresol purple, while A3-1-1-2-1-1-1-2 remained relatively free from it. There were similar differences in the absorption of color on media containing methyl red, methyl orange, gentian violet, and litmus.

Growth on standard bacteriologic media.—Because of these preliminary indications of physiologic differences between different mutant lines, it was decided to make a more intensive study of a few lines. The following, all derivatives from W. Va. A8, were selected: A8-1-1, A8-5-2-1, A8-5-3-2-5, A8-5-4, A8-3-1, A8-5-3-3-2, A8-5-5, A8-5-1-3-3, A8-5-1-2, A8-5-1, A8-5-1-6, and A8-5-7-1. First they were grown on standard bacteriological media to find out whether there were decided differences in behavior. The media were prepared according to the methods recommended by the Society of American Bacteriologists (16). The reaction of all media except milk was adjusted to pH 7 with NaOH, using brom-thymol blue as indicator.

All 12 lines grew slowly on solid media containing beef extract and peptone, attaining a diameter of only 3 to 6 mm. in two weeks. In virtually all cases the outline of the colony on beef extract media was irregular, the color white or creamy, and the surface either powdery or wet shiny.

In peptone broth and peptone alone there was considerable variety in the type of growth produced by the different mutants. All except one produced at least some surface growth, but there were considerable differences in the amount. This surface growth usually was present in the form of small particles of various sizes floating on the surface, rather than as a complete pellicle or ring. The surface growth of some mutants was moist on top while that of others was dry and powdery. In some cases the medium was turbid because of the presence of very fine aggregations of mycelium or sporidia; in others it was clear except for small flocculae. Usually there was some sediment, the amount varying with the different mutants. W. Va. A8-5-3-1-2 was unique in the fact that it produced no surface growth, and the liquid was perfectly clear except for the presence of abundant fluffy masses at the bottom of the tube.

A positive test for indol could not be obtained when the organism was grown on peptone. Neither was the odor of the broth nor of the peptone changed.

According to Levine and Carpenter (38), bacteria can be divided into three classes by their effect on gelatin: (1) those that do not hydrolyze; (2) those that partially hydrolyze and liquefy gelatin, with subsequent decomposition slow, if any; (3) those that completely hydrolyze and liquefy gelatin, with subsequent rapid decomposition.

Decomposition of the gelatin was based on formol titration of amino groups.

Ustilago zeae falls into the third class because all of the mutants studied reduced gelatin to a fluid of relatively low viscosity. There were, however, significant differences in the rates at which different lines caused liquefaction. Except in the case of two lines, liquefaction was complete a definite distance from the top, and the boundary between liquid and solid was very distinct for these lines. In Table IX are summarized the data for 12 lines grown for 12 days in triplicate flasks at 18°C. It is apparent by comparing the data in Table IX with those in Table XIV that, altho some mutant lines grew well at 18°C., they did not liquefy gelatin rapidly at that temperature. Evidently, therefore, temperature is not the limiting factor, but the differences in liquefaction are due to the differential ability of the smut lines to grow on gelatin and to produce gelatin-liquefying enzymes.

TABLE IX

Type of Growth and Amount of Liquefaction Produced by Mutant Lines of W. Va. A8 Grown for Twelve Days on Gelatin at 18°C.

Mutants	Depth of liquefaction in mm.	Description of growth
A8-1-1	14-15	Medium growth on surface and at boundary between liquid and solid
A8-5-2-1	10	Medium growth on surface and at boundary between liquid and solid
A8-5-3-2-5	12-15	Abundant growth at surface and at liquid-solid boundary; tendency for mycelium to float in medium
A8-5-4	Very little	Surface growth slight
A8-3-1	11	Abundant surface growth; moderate growth at liquid-solid boundary
A8-5-3-3-2	Very little	Slight surface growth
A8-5-5	15	Moderate growth at surface and at liquid-solid boundary
A8-5-1-3-3	20	Liquefaction complete about 10 mm. deep and then a crater-shaped hole, 10 mm. deep
A8-5-3-1-2	38-40	Liquefaction nearly complete except for a little at the bottom and an irregular shaped piece 15 mm. long along one side.
A8-5-1	25	Growth moderate at surface and at liquid-solid boundary; boundary even except in one case where the submerged inoculum near the boundary started to grow
A8-5-1-6	15	Abundant growth on surface; medium growth at liquid-solid boundary
A8-5-7-1	15	Medium growth on surface and at liquid-solid boundary

Skim milk was first slightly coagulated by the cultures, probably by chymase, as there was no apparent change in acidity. The casein was digested later, leaving the milk translucent and light yellow in

TABLE X

RELATIVE RATE OF DIGESTION OF CASEIN BY MUTANTS OF W. VA. A8 AS MEASURED BY THE SIZE OF THE COLONIES AND OF THE CLEARED AREA AFTER HAVING GROWN ON MILK AGAR FOR NINE DAYS AT ROOM TEMPERATURE

Mutants	Flask No.	Experiment 1		Experiment 2		Mutants	Flask No.	Experiment 1		Experiment 2	
		Diameter in mm.		Diameter in mm.				Diameter in mm.		Diameter in mm.	
		Colony	Clear area	Colony	Clear area			Colony	Clear area	Colony	Clear area
A8-1-1	1	14	36	18	41	A8-5-5	1	19	40	21	44
	2	10	30	15	36		2	19	40	21	43
	3	14	37	16	38		3	18	38	21	43
	4	..	..	15	36		4	..	..	21	43
A8-5-2-1	1	14	17	12	15	A8-5-1-3-3	1	20	45	21	43
	2	14	19	12	14		2	19	44	22	46
	3	15	17	12	14		3	19	44	22	44
	4	..	..	12	15		4	..	..	21	43
A8-5-3-2-5	1	19	40	*	*	A8-5-3-1-2	1	12	37	15	47
	2	21	42	23	47		2	12	37	*	*
	3	19	40	22	45		3	15	42	13	42
	4	..	..	21	44		4	..	..	15	47
A8-5-4	1	17	30	18	36	A8-5-1	1	17	41	20	44
	2	15	29	18	34		2	18	43	†	†
	3	17	31	17	31		3	19	43	20	44
	4	..	..	18	34		4	..	..	18	42
A8-3-1	1	19	41	22	43	A8-5-1-6	1	15	37	14	35
	2	19	42	21	41		2	14	37	14	35
	3	19	40	21	41		3	14	37	13	34
	4	..	..	21	41		4	..	..	14	35
A8-5-3-3-2	1	14	27	17	22	A8-5-7-1	1	14	38	18	39
	2	16	32	17	27		2	14	37	18	39
	3	14	27	18	29		3	14	37	17	36
	4	..	..	17	21		4	..	..	18	39

* Contaminated.

† No growth.

color. There was some surface growth in the case of all lines, but the amounts differed. Usually there was a ring pellicle at first, which later extended and covered the entire surface.

Digestion of casein.—It was observed in the foregoing experiments that different mutant lines digested casein at different rates. In order better to study these differences, milk was incorporated into a solid medium prepared as follows: 25 cc. distilled water plus 2½ per cent agar poured into 250 cc. Erlenmeyer flasks and sterilized under 15 pounds of steam pressure. While the agar was still hot, 15 cc. of milk was added to each flask, using aseptic technique. In order to avoid caramelizing the milk sugar and precipitating the albumins, the flasks were heated in an Arnold sterilizer for 20 minutes, after which they were taken out and allowed to cool. The resulting medium was pure white and homogeneous. The flasks were then inoculated in triplicate or quadruplicate with each mutant line. As early as one day after inoculation a yellowish translucent area began to appear around the colonies. This area approximated a definite circle in form and was of fairly definite size for each mutant line. Apparently the enzyme produced by the fungus diffused through the gel and evidently was produced in different amounts by different lines. The size of the colonies and of the digested areas are given in Table X. Results seemed to indicate rather clearly that there are decided differences in the ability of the different lines to digest the casein in the milk.

TABLE XI

RATIOS OF THE AREA OF MILK AGAR DIGESTED BY MUTANTS OF W. VA. A8 TO THE AREA OF THE COLONY, NINE DAYS AFTER INOCULATION

Mutants	Clear area / Colony area		Mutants	Clear area / Colony area	
	Experiment 1	Experiment 2		Experiment 1	Experiment 2
A8-1-1	7.53	6.00	A8-5-5	4.44	4.24
A8-5-2-1	1.47	1.40	A8-5-1-3-3	5.26	4.49
A8-5-3-2-5	4.28	4.56	A8-5-3-1-2	8.95	10.02
A8-5-4	3 36	3.78	A8-5-1	5.54	5.04
A8-3-1	4.65	3.68	A8-5-1-6	6.52	6.28
A8-5-3-3-2	3.81	2.08	A8-5-7-1	6.93	4.64

This apparently is due to differential ability to produce proteolytic enzymes, as there was no correlation between the size of the colony and the surrounding area in which the casein was digested. (See Table XI and Plate V.) Amino acid determinations were made by the Vanslyke method and indicated that the protein actually was digested, but the comparative results obtained by the method were so variable that it seems possible that the digestion was not carried to the same stage by all lines.

Similar differences in the ability of certain fungi to produce enzymes have been noted by Currie and Thom (17), who showed that the ability of different strains of Penicillium to produce oxalic acid differed considerably. Oshima and Church (40) found that strains of *Aspergillus* of the flavus-oryzae group differed considerably in the amount of protease and amylase which they were able to produce, and Letcher and Willaman (37) showed that physiologic forms of *Fusarium lini* differed with respect to alcohol production.

Effect on sugars.—No gas was formed nor were there any apparent changes in pH when the cultures were grown on various pure carbohydrates as the only source of carbon. A liquid medium was used containing KH_2PO_4, KCl, $MgSO_4$, plus the particular carbohydrate to be tried, as recommended by the Society of American Bacteriologists (16) for use in detecting small changes in pH. The following carbohydrates were used: l-xylose, d-mannitol, d-levulose, and maltose. The medium was sterilized in the Arnold sterilizer in order to avoid changes in the sugars. Brom-thymol blue was used as indicator.

All 12 mutants grew well on each of the 4 carbohydrates, altho they grew slightly better on maltose than on any of the other 3. There was no visible change in the color of the indicator; neither did gas collect in the gas traps placed in the tubes.

Reduction of nitrates and iodine.—The ability to reduce nitrates to nitrites is characteristic of many bacteria and is used as one of the criteria of identification. In preliminary experiments with *U. zeae* grown on solid media containing KNO_3, it was found that if iodine was added to the medium several days after inoculation it was either absorbed or reduced near the mycelial mat, and no longer gave a blue color with starch. It was thought that this might be due to the reaction of the iodine with the nitrites formed in the medium. The following experiment was therefore made. Each of the 12 lines listed in Table XII was grown on 8 flasks of solid medium, 6 of which contained agar, starch, sucrose, $MgSO_4$, K_2HPO_4, and KNO_3. In the other 2 the KNO_3 was omitted.

Five days after inoculation the flasks containing the KNO_3 gave a strong test for nitrites with sulphanilic acid and alpha-naphthylamine. Ten days after inoculation, 2 cc. of a saturated solution of iodine in 50 per cent alcohol was added to 2 flasks of each line growing on the medium containing KNO_3, as well as to those which contained none. Colorless circular areas, of different size for each line, appeared on the KNO_3 media. When more iodine was added, the typical blue color reappeared, indicating that the iodine and not the starch was affected. The iodine was reduced slightly and slowly in the medium containing no nitrate. Thirteen days after inoculation iodine was added to the remaining 2 flasks of each line containing the nitrite.

Several lines, one in particular, caused vigorous reduction of the iodine, while others reacted very slightly. The result is hard to account for, but it is possible that some of the lines used up large amounts of nitrate for further growth. Comparative data are given in Table XII, and the appearance is shown in Plate VI. The results seemed to indicate that much of the reduction of iodine was due to nitrites produced by the fungus through the reduction of nitrates. Apparently another substance that causes the disappearance of the iodine-starch color is produced in small amounts, as indicated by the slow clearing of media containing no nitrates.

TABLE XII

DIFFERENCES IN PRODUCTION OF IODINE-REDUCING SUBSTANCES BY MUTANTS OF W. VA. A8, AS MEASURED BY DIAMETER OF COLONY AND OF THE CLEAR AREA

Mutants	Flask	Medium, treatment, and diameters of colonies in mm.					
		Iodine added 10 days after inoculation				Iodine added 13 days after inoculation	
		KNO$_3$ in medium Diameter in mm.		No KNO$_3$ in medium Diameter in mm.		KNO$_3$ in medium Diameter in mm.	
		Colony	Clear area	Colony	Clear area*	Colony	Clear area
A8-1-1	1	10	19	7	10	12	21
	2	9	19	7	10	14	26
A8-5-2-1	1	14	15	10	+	12	0
	2	10	11	10	+	12	0
A8-5-3-2-5	1	14	18	16	+	19	0
	2	13	17	16	+	19	0
A8-5-4	1	13	20	14	12	19	19
	2	13	18	13	11	19	19
A8-3-1	1	16	34	17	14	23	65
	2	14	27	15	13	24	72
A8-5-3-3-2	1	12	16	13	13	17	20
	2	13	18	14	14	18	21
A8-5-5	1	18	22	17	+	24	26
	2	17	21	18	+	25	27
A8-5-1-3-3	1	15	15	18	+	25	0
	2	15	15	18	+	27	0
A8-5-3-1-2	1	12	15	11	+	15	15
	2	12	13	13	+	16	16
A8-5-1	1	13	14	16	++	20	20
	2	..	..	15	++	20	20
A8-5-1-6	1	8	16	7	7	10	14
	2	7	15	8	8	9	12
A8-5-7-1	1	15	15	19	—	19	19
	2	14	14	19	—	18	18

* + = clear area barley discernible; ++ = stronger than + but still too small to measure; — = no action.

Fellenberg and Geilinger (21) state that *Aspergillus niger* is able to take up elemental iodine, but they attributed the action to a binding of the iodine by the proteins in the fungus. It is apparent, however, that the iodine-reducing substance produced by *U. zeae* is able to diffuse away from the culture through the agar gel.

The blue color gradually disappeared from uninoculated control flasks about 10 or 12 days after the iodine was added. It was thought that this might be due to the fact that sucrose had become inverted when sterilized in the presence of K_2HPO_4. The action in this case, however, is too slow to compare with the above described phenomenon, which appeared within a few hours. Furthermore, the iodine would not disappear in a circular area under such circumstances.

It is significant that the rate of action of the different lines on iodine differs greatly. W. Va. A8-3-1 was outstanding in that it cleared the iodine much more rapidly than did the other lines and also left the medium with a reddish tinge after the iodine-starch color had disappeared. This condition was not observed in cultures of any other lines. While the results of these experiments cannot be explained fully, they do indicate clearly that there are quantitative physiologic differences between mutants of *U. zeae*.

Temperature relations.—It is known that physiologic forms of several fungi may have different temperature requirements. This has been shown by Edgerton (20) for forms of *Glomerella cingulata;* by Hursh (27) for forms of *Puccinia graminis tritici;* by Rodenhiser (42) for forms of *Ustilago nuda, U. tritici,* and *U. hordei;* and by Harter and Weimer (25) for strains of *Rhizopus nigricans.* Johnson (28) also reported that one form of *Helminthosporium gramineum* grew much better at low temperature than did another form of this species.

TABLE XIII

EFFECT OF TEMPERATURE ON THE RATE OF GROWTH OF MUTANTS OF W. VA. A8, AS MEASURED BY THE AVERAGE DIAMETERS OF DUPLICATE COLONIES GROWN FOR 16 DAYS ON POTATO-DEXTROSE-MALT AGAR*

Mutants	Temperature, and diameters of colonies in mm.†			
	10° C.	18° C.	26° C.	34° C
A8-1-1	4	19	13	16
A8-5-2-1	22	28	29	24
A8-5-3-2-5	7	21	26	24
A8-5-4	5	21	25†	6
A8-3-1	8	31	32	11
A8-5-3-3-2	10	24	35	19
A8-5-5	7	22	33	18‡
A8-5-1-3-3	10	25	31	28
A8-5-3-1-2	10	23	24	12
A8-5-1	6	23	29	15
A8-5-1-6	5	8	17	22
A8-5-7-1	6	19	33	18

* All flasks kept for 48 hours at room temperature, after which they were kept for two weeks at the various temperatures.

† Fractions counted as nearest whole number.

‡ Only one colony measured.

There were outstanding differences in the temperature requirements of the mutant lines of *U. zeae* listed in Table XIII. These lines were grown on potato-dextrose agar containing potato extract, 1 per cent dextrose, 1 per cent sucrose, and 1 per cent by weight of Trommer's malt syrup. Duplicate Erlenmeyer flasks, each containing 32 cc. of this medium, were inoculated with each line, and kept at room temperature for 48 hours, after which they were placed at 10°, 18°, 26°, and 34°C., respectively. At the end of 14 days at these temperatures the diameters of the colonies were measured in two directions at right angles to each other, and the results averaged. This was particularly necessary in this case because of the fact that at some temperatures the outlines of colonies are irregular rather than circular. The results are given in Table XIII.

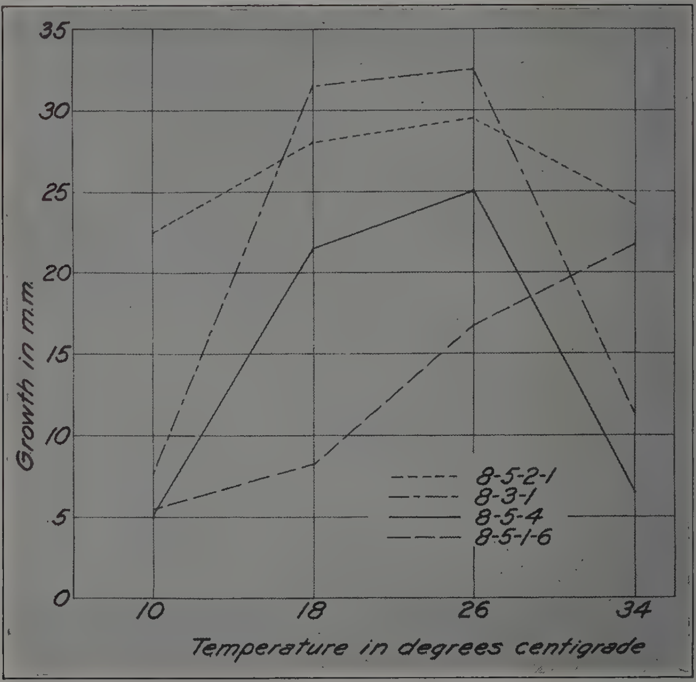

Fig. 6. Chart showing rate of growth as indicated by diameter of colonies of four mutants derived from *U. zeae* W. Va. A8, grown for 14 days at different temperatures.

It will be seen from Table XIII that W. Va. A8-5-2-1 grows well at a wide range of temperature, whereas A8-3-1 and A8-5-4 grew only very slowly at the extremes. A8-5-1-6 appears to have a higher optimum than any of the others. Not only was the size of colonies greatly influenced by temperature, but there were decided differences in the topography. There was a decided tendency for colonies of A8-5-2-1 and A8-3-1 to curl up away from the medium at the lower temperatures. At high temperatures, on the other hand, cultures of these lines were very closely appressed to the agar, and even cracked it in some cases and then grew into the cracks. (See Fig. 6.)

The results confirm the large number of miscellaneous observations to the effect that temperature profoundly affects the rate of growth, the final size and appearance of colonies, and that this effect varies with different mutant lines of *U. zeae*.

These experiments also furnish additional evidence that mutant lines of *U. zeae* differ in physiologic characters, some of the most outstanding of which are: ability to liquefy gelatin, digest casein, reduce nitrates and iodine; and in temperature relations.

Morphology of Sporidia

It already has been pointed out that there may be mutations in type of growth. Lines characterized by the mycelial type of growth may produce mutants which are predominantly sporidial and vice versa. As pointed out previously, there are all gradations between mycelial and sporidial types. It was noted also that the sporidia of some mutants differed decidedly from those of their parents and other mutants in shape and size, when grown under the same conditions. For example, Texas A is easily distinguished from Minn. A by its larger, blunt-ended sporidia. It seemed likely that there might be consistent differences in the morphology of sporidia of different mutants from the same parent. Therefore the question was investigated.

TABLE XIV

Size, Shape, and Color of Sporidia of Minn. A and Three of Its Mutant Derivatives Grown in a Solution of 1 Per Cent Gelatin and 2 Per Cent Dextrose for 14 Days

Lines	Length (in microns)	Character of surface growth and of sporidia
Minn. A	13.0	Sporidia regular, hyaline, usually fusiform; growth on medium, tan colored
Minn. A-3-1-2	9.7	Similar to the above, but sporidia usually more blunt; a distinctly white growth on the medium
Minn. A-4-4-5	13.7	Sporidia of two types, regular or irregular, frequently dumbbell in shape; growth slightly lighter in color than that of parent
Minn. A13	15.1	Sporidia mostly irregular, of various shapes, often simulating chlamydospores; growth on the medium dark

Three mutants, Minn. A3-1-2, Minn. A4-4-5, and Minn. A13, and the parent, 16 Minn. A, were grown in a liquid medium consisting of 1 per cent gelatin and 2 per cent dextrose in distilled water. The sporidia were examined after the cultures had grown for two weeks. The usual precautions were taken to select a random sample of sporidia for measurement, all of those encountered in passing from one end of the mount to the other being measured. It was considered that 98 spores would constitute a fair random sample of the populations studied. The results are summarized in Table XIV.

It seems evident from Table XIV that the sporidia of some of the mutants of Minn. A differ from those of the parent and from those of other mutants. Those of Minn. A3-1-2 appeared to be shorter than those of the parent, while those of Minn. A13 appeared longer. The most conspicuous difference in morphology was the production of dumbbell-shaped sporidia of Minn. A4-4-5. Minn. A13 produced sporidia which could easily be distinguished from those of the other lines because they were darker in color and frequently resembled immature chlamydospores. This experiment was repeated two months later under conditions similar to those of the first test. The results with respect to shape of sporidia corresponded closely with those obtained in the first experiment.

It is difficult to make experiments on morphology of sporidia under conditions that are rigidly enough controlled to justify drawing final conclusions. This is owing to the fact that many lines mutate so frequently that very careful precautions must be taken to exclude mutants from the cultures that are to be studied. This is especially true when the cultures are grown in liquid media, in which mutation cannot be observed directly. Nevertheless, the authors are convinced that consistent differences in the morphology of the sporidia come about as a result of mutation. Thus, sporidia of some of the mutants from W. Va. A8 were narrowly fusiform, others cylindrical, and others ovoid. The color, also, differed greatly under certain conditions. Sporidia of some lines were distinctly hyaline, others somewhat olivaceous, and still others almost fuliginous. As a matter of fact, one would scarcely recognize the sporidia of some mutants as those of *U. zeae*.

Pathogenicity and Sex

Sex and pathogenicity are to a considerable extent interdependent in *U. zeae*, as normal infection of the corn plant usually results from the growth of the dikaryophase in the corn tissues. According to Hanna (24), the haploid hyphae from germinating sporidia can penetrate the tissues; but ordinarily smut galls and chlamydospores are not formed unless two hyphae of opposite sex fuse and give rise to a binucleate mycelium (24, 44). Apparently most monosporidial lines, alone, cannot cause the disease, altho it will be shown in Part II of this bulletin that a few can. These monosporidial lines are the only entities that can be propagated independently and the only ones in which mutations in sex and pathogenicity can be studied. But so far it has been necessary to study both by observing the behavior of a line in combination with others. The study of the pathogenic characters of mutants would be simpler, therefore, if the pathogene were not predominantly heterothallic.

The problem is complicated further because there are more than two sexual groups, with varying degrees of sexual compatibility, that is, multiple factors for sex; consequently it is difficult to know to what extent pathogenicity is merely a function of sex factors and to what extent a function of the physicochemical attributes of the haploid lines that unite to produce the pathogenic phase of the fungus. Gall formation is closely associated with chlamydospore production, and degrees of pathogenicity conceivably may depend largely on the complement of sex factors carried by the dikaryons and diplonts. On the other hand, haploid lines do differ in physiologic characters, and it seems probable that they may have varying degrees of virulence also. In addition, some lines mate perfectly well and produce normal chlamydospores without, at the same time, producing galls as large as those produced by other combinations of lines, thus furnishing evidence that pathogenicity is not solely a function of sex compatibility.

Whatever the ultimate factors for virulence may be, the degree of pathogenicity depends to a considerable extent on sex; hence changes in sex are accompanied by changes in pathogenicity. If a line that can unite readily with several other lines produced rapidly growing and prolific mutants that can unite with fewer lines, the potential pathogenicity of the pathogene has been decreased. The converse might also be true. Until more precise information becomes available, it seems best to consider sex and pathogenicity together.

Blakeslee (3, 4), Kniep (33), and Derx (18) observed change of sex (usually loss of sex factors) in *Mucor*, *Schizophyllum*, and *Penicillium*, respectively, after they had been grown for some time in artificial culture. This phenomenon is common in *U. zeae* also. Some of the most vigorous lines, sexually, have lost their power to unite with lines of opposite sex, but in every case the line in which such a change occurred was known to mutate frequently, at least under some conditions.

Christensen (13) stated that in the case of *Helminthosporium sativum* there were mutations in the pathogenic capabilities of certain forms. The mutants usually were less virulent than the parent, but some were more virulent. Stakman, Christensen, and Hanna (45), and Hanna (24) called attention to apparent change in sexual reaction and pathogenicity of some mutants of *U. zeae*. Further experiments were made by the authors.

The method of preparing inoculum and inoculating the plants was essentially that described by Stakman and Christensen (44). The lines were grown separately in a solution of 2 per cent dextrose and 1 per cent malt syrup. They were allowed to grow for two or three weeks before inoculations were made. The cultures were then mixed just before inoculation and the inoculum injected into the plants by means of a hypodermic syringe, as near the growing point as possible. The controls were always inoculated in like manner with sterile nutrient solution and with monosporidial cultures.

Results of inoculations with certain mutant lines from Minn. A are summarized in Tables XV and XVI. It will be noted that there were pronounced differences in the parasitic power of some of the mutants, as compared with that of their parents and other mutants.

TABLE XV

RESULTS OF INOCULATING CORN IN THE GREENHOUSE WITH SEVEN MUTANTS OF MINN. A IN COMBINATION WITH THEIR PARENT AND WITH THREE OTHER MONOSPORIDIAL LINES OF KNOWN SEX[*]

Lines		No. plants inoculated	No. plants with galls	Severity of infection
Minn. A1-1	x Minn. A	48	0	....
do	x Minn. F	0	..	....
do	x Minn. D	37	2[†]	Warts
do	x Canada A	46	14[‡]	Slight; 2 large galls
Minn. A3	x Minn. A	25	0	....
do	x Minn. F	25	20	Moderate
do	x Minn. D	27	24	Moderate
do	x Canada A	29	24	Moderate
Minn. A3-1	x Minn. A	32	0	....
do	x Minn. F	0	..	....
do	x Minn. D	29	24	Heavy
do	x Canada A	33	31	Heavy
Minn. A4-2	x Minn. A	46	0	....
do	x Minn. F	58	56	Heavy
do	x Minn. D	59	49	Moderate
do	x Canada A	51	36	Moderate
Minn. A4-7	x Minn. A	30	0	....
do	x Minn. F	0	..	....
do	x Minn. D	38	28	Heavy
do	x Canada A	20	18	Heavy
Minn. A6	x Minn. A	15	0	....
do	x Minn. F	0	..	....
do	x Minn. D	13	10	Moderate
do	x Canada A	13	12	Heavy
Minn. A10	x Minn. A	22	0	....
do	x Minn. F	0	..	....
do	x Minn. D	22	16	Light
do	x Canada A	37	19	Light
Minn. A12	x Minn. A	60	0	....
do	x Minn. F	53	45	Heavy
do	x Minn. D	65	52	Heavy
do	x Canada A	54	44	Heavy
Minn. A13	x Minn. A	60	0	....
do	x Minn. F	60	57	Heavy
do	x Minn. D	62	56	Heavy
do	x Canada A	51	40	Heavy
Minn. A	x all mutants	31	0	....
do	x Minn. F	62	39	Heavy
do	x Minn. D	60	51	Heavy
do	x Canada A	53	47	Heavy

[*] Four selfed lines of corn as well as Golden Bantam were inoculated but variations in degree of infection on the different lines were not very great. The results, therefore, are included together.

[†] Formation of chlamydospores doubtful.

[‡] Two large galls near base of plant, perhaps due to contamination.

TABLE XVI

RESULTS OF INOCULATING GOLDEN BANTAM SWEET CORN AND GEHU CORN WITH MINN. A AND FOUR OF ITS MUTANTS IN COMBINATIONS WITH FIVE OTHER LINES OF *Ustilago zeae*[*]

Lines	No. plants inoculated	No. plants infected	Degree of infection
Minn. A x Minn. F	15	15	Heavy
do x Canada A	16	14	Heavy
do x Minn. B	14	14	Heavy
do x Minn. C	..	..	....
do x Minn. D	15	14	Heavy
Minn. A1-1 x Minn. F	12	0	....
do x Canada A	16	2	Warts only
do x Minn. B	13	6	Moderate
do x Minn. C	15	0	....
do x Minn. D	14	1	One large gall[†]
Minn. A3-1-1-2-1-1 x Minn. F	15	12	Moderate
do x Canada A	15	11	Moderate
do x Minn. B	18	12	Moderate
do x Minn. C	16	0	....
do x Minn. D	17	16	Heavy
Minn. A4-4-5 x Minn. F	8	8	Heavy
do x Canada A	16	1	Light
do x Minn. B	11	9	Heavy
do x Minn. C	..	..	....
do x Minn. D	18	13	Heavy
Minn. A13 x Minn. F	17	17	Heavy
do x Canada A	15	3	Light
do x Minn. B	17	16	Heavy
do x Minn. C	14	0	....
do x Minn. D	16	11	Heavy

[*] Reactions of two varieties were approximately the same; the results therefore are combined.

[†] Gall near base of plant perhaps due to contamination.

It is apparent from Table XV that Minn. A unites normally with lines of opposite sex, Minn. F, Minn. D, and Canada A, producing heavy infection. Obviously, none of the mutants could do better on the lines of corn used in the experiment. Many did not do so well as the original parent, indicating a loss of virulence by mutation, which one would expect. But it seems clear that some mutants may be more virulent than their immediate parent. This is shown by the fact that Minn. A3 caused only moderate infection in combination with Minn. D and Canada A, while Minn. A3-1 caused heavy infection with these same lines. The virulence of this mutant exceeded that of its immediate parent, but not that of its "grandparent." This could hardly be expected of it, however, as the "grandparent" already had the maximum virulence for the variety of corn inoculated.

Mutants clearly may differ from each other in pathogenicity and sex, indicating that mutations in these characters occur (Table XV). One of the most striking changes that has been observed was in Minn. A13. This line produced heavy infection with Minn. F, Minn. D, and Canada A. (See Table XV.) When experiments were made nine months later, however, Minn. A13 produced only light infection with Canada A. The experiments were repeated, but the differences remained constant. At present A13 is only weakly parasitic with Minn. F also, indicating a change in virulence, but not a complete change in sex factors.

Mutants were paired within their parents (Tables XV, XVII) and in no case did they unite, indicating that the sex had not changed completely by mutation. There are differences in virulence, however, as can be seen by a perusal of Tables XV and XVI.

TABLE XVII

Results of Inoculating Minn. No. 13 Corn with W. Va. A8 in Combinations with Six of Its Mutant Derivatives, and with Two of Its Mutant Derivatives and One Sister Mutant in Combinations with the Same Six Mutants

Lines	A8	A8-5	A8-5-1	A7
A8	..	..	$\frac{0}{15}$*	..
A8-5-1	$\frac{0}{15}$	$\frac{0}{21}$	$\frac{0}{18}$	$\frac{0}{18}$
A8-5-1-1	$\frac{0}{17}$	$\frac{0}{21}$	$\frac{0}{16}$	$\frac{0}{17}$
A8-5-1-2	$\frac{0}{18}$	$\frac{0}{18}$	$\frac{0}{20}$	$\frac{0}{17}$
A8-5-1-6	$\frac{0}{20}$	$\frac{0}{24}$	$\frac{0}{19}$	$\frac{0}{20}$
A8-5-1-7	$\frac{0}{19}$	$\frac{0}{18}$	$\frac{0}{18}$	$\frac{0}{15}$
A8-5-1-8	$\frac{0}{17}$	$\frac{0}{21}$	$\frac{0}{19}$	$\frac{0}{23}$

* Denominator = number plants inoculated; numerator = number plants infected.

In Table XVIII are recorded the results of inoculating Minn. No. 13 corn and Gehu with W. Va. A8-5-1, its immediate mutant, A8-5-1-1, and six mutants from the latter. It is apparent that A8-5-1-1-3a and A8-5-1-1-5a were less virulent than both of the above-mentioned on both varieties of corn inoculated. On the other hand, A8-5-1-1-6 seems more virulent on Gehu, both with Minn. E and Italy A1, than its immediate parent. The same appears to be true of A8-5-1-1-7. There are indications, therefore, that there may be a certain degree of specificity of certain combinations of smut lines for certain varieties of corn; and there is further evidence that mutants may be either more or less virulent than their parents.

TABLE XVIII

RESULTS OF INOCULATING TWO VARIETIES OF CORN WITH W. VA. A8-5-1 AND SEVEN OF ITS MUTANT DERIVATIVES IN COMBINATIONS WITH MINN. E AND ITALY A1

Lines	Smut lines, corn varieties, and degree of infection*			
	Minnesota E		Italy A1	
	Minn. 13	Gehu	Minn. 13	Gehu
A8-5-1	$\frac{6^3}{9}$ M ±	$\frac{5}{5}$ L ±	$\frac{2^6}{11}$ M ±	$\frac{1}{10}$
A8-5-1-1	$\frac{11}{11}$ M ++	$\frac{5}{5}$ S ±	$\frac{1^2}{9}$ M ±	$\frac{4}{5}$ S +
A8-5-1-1-2a	$\frac{11}{11}$ M to L +++	$\frac{6}{6}$ M to L +++	$\frac{11}{13}$ M to S ++	$\frac{6}{7}$ S to M +
A8-5-1-1-3a	$\frac{4^6}{13}$ M +	$\frac{3^4}{7}$ VS −	$\frac{2^8}{11}$ S ±	$\frac{0}{5}$
A8-5-1-1-5a	$\frac{5}{5}$ S +	$\frac{8^7}{15}$ S to M ±	$\frac{4}{7}$ S ±	$\frac{11}{13}$ S to M +
A8-5-1-1-6	$\frac{5}{6}$ M ++	$\frac{13}{13}$ S to L +++	$\frac{6}{6}$ M +++	$\frac{13}{13}$ M to L +++
A8-5-1-1-7	$\frac{3}{4}$ M +++	$\frac{11}{12}$ VL ++	$\frac{5}{7}$ S ++	$\frac{13}{14}$ L +++
A8-5-1-1 8	$\frac{6}{7}$ M ++	$\frac{12}{13}$ M +	$\frac{\text{[illegible]}}{7}$ S ±	$\frac{8}{11}$ S to M +

* The denominator denotes the number of plants inoculated and the numerator the number on which galls were produced . The exponent numbers indicate the number of plants on which incipient galls were produced.

L = large galls.
VL = very large galls.
M = medium sized galls.
S = small galls.
VS = very small galls.

+++ = very many galls.
++ = many galls.
+ = moderate number of galls.
± = few galls.
— = very few galls.

Table XIX summarizes the results of inoculating Golden Bantam corn with W. Va. A8 and a number of its mutant descendants in combinations with several other lines. A8-1-1 is at least equally as virulent as the parent, and possibly more so, but the other three are less virulent in all combinations. It appears that A8-5-5 and A8-5-3-1-2 are considerably less virulent than W. Va. A8, altho they have not completely lost the power to unite with those lines with which A8 unites, except perhaps with Italy A1. Even A8 does not form a virulent combination with Italy A1. It will be noted that A8 is only weakly parasitic with Minn. C, also. W. Va. A8-5-3-3-2 seems to be entirely unable to unite with any of the lines with which it was mated, apparently being entirely devoid of the necessary sex factors.

The results again show that some mutant lines form virulent combinations with certain other lines and only very weakly parasitic combinations with others. They also show that mutation may result in changes in sexual and pathogenic powers. A8-5-5 and A8-5-3-1-2 may have lost certain factors for sex, as relatively few chlamydospores were produced, or it may be that the dikaryophytes were unable to grow well in the tissues of the host because factors for physiologic vigor were absent. Either interpretation would seem plausible, but further studies must be made before drawing final conclusions. W. Va. A8-5-3-3-2 probably has lost the sex factors of the parent and has become sterile, or it is of different sex, as it failed to form chlamydospores or to produce clearly visible indications of infection with any of the lines with which it was paired.

TABLE XIX

Results of Inoculating Corn with W. Va. A8 and Four of Its Mutant Derivatives in Combinations with Eight Other Monosporidial Lines

Lines	Smut lines and degree of infection*				
	W. Va. A8	W. Va. A8-1-1	W. Va. A8-5-5	W. Va. A8-5-3-1-2	W. Va. A8-5-3-3-2
Minn. A	$\frac{11}{12}$ M +	$\frac{10}{10}$ M ++	$\frac{7}{11}$ I to S —	$\frac{3}{13}$ I to S —	$\frac{0}{15}$
Minn. C	$\frac{4}{12}$ I to S ±	$\frac{4}{11}$ I to S ±	$\frac{2}{14}$ I	$\frac{3}{15}$ I	$\frac{0}{11}$
Minn. E	$\frac{11}{12}$ M +	$\frac{13}{13}$ L +++	$\frac{5}{10}$ I	$\frac{0}{11}$	$\frac{0}{14}$
Spain A	$\frac{11}{12}$ L +++	$\frac{13}{14}$ L +++	$\frac{4}{11}$ I to S —	$\frac{3}{11}$ I to S —	$\frac{0}{13}$
Italy A1	$\frac{9}{11}$ I to S ±	$\frac{8}{10}$ M +	$\frac{0}{11}$	$\frac{0}{12}$	$\frac{0}{11}$
Minn. A13 x Minn. F.5†	$\frac{11}{11}$ L +++	$\frac{13}{14}$ M ++	$\frac{7}{11}$ I	$\frac{6}{10}$ I to S —	$\frac{0}{13}$
Minn. A13 x Minn. F.8	$\frac{15}{15}$ M +++	$\frac{12}{13}$ L +++	$\frac{3}{11}$ I	$\frac{6}{13}$ I to S —	$\frac{0}{10}$
Minn. A13 x Minn. F.10	$\frac{16}{17}$ L +++	$\frac{11}{12}$ L +++	$\frac{5}{11}$ I to S —	$\frac{0}{14}$	$\frac{0}{10}$

* The denominator denotes the number of plants inoculated and the numerator the number on which galls were produced.

L = large galls.
M = medium sized galls.
S = small galls.
I = incipient galls.

+++ = very many galls.
++ = many galls.
+ = moderate number of galls.
± = few galls.
— = very few galls.

† Minn. A13 x Minn. F.5, etc., = fifth sporidium from the cross indicated.

Mutations in sex and pathogenicity evidently occur commonly and may result either in gain or in loss of factors, apparently for both characters, altho loss seems more common than gain. It appears evident that there may be various degrees of loss of virulence and sexual power in mutants from the same monosporidial line. The authors are of the opinion that, in *U. zeae* at least, the loss of virulence in culture is due to mutation, as the changes of this nature that they observed were sudden, not gradual. Furthermore, there is positive evidence that there is not necessarily a correlation between the virulence and sexual vigor of a monosporidial line and the length of time it has been grown in artificial culture. Minn. E and Minn. F have, for example, been in culture for four years and have lost neither sexual nor pathogenic potency. These lines do not mutate frequently; consequently it is relatively easy to maintain their purity. But this is not true of the lines that mutate freely, and it was in such lines that the authors observed most of the so-called loss of sex and pathogenicity. Sex mutations would be observed less easily than mutations resulting in such easily observable characters as color, type of growth, etc. In fact, the only way to determine them would be by inoculations, unless the mutants happened to differ in appearance. Using ordinary mycological culture routine, there is no assurance that a culture will remain the same after several successive transfers as it was at the beginning. Care must be taken to transfer each time from the parent, and not from the parent plus one or more mutants, or from mutants alone. Changes in pathogenicity of a culture do occur; but not by gradual degradation due to growth on artificial media, at least so far as the authors' observations go. Unless necessary precautions are taken to transfer continually from the original line, the culture is likely to comprise several lines after relatively few "cultural generations," and none of these may be the same as the original, which easily may have been lost in transferring cultures by ordinary methods. A true explanation of loss of pathogenicity might be that the pathogenic line was lost in the shuffle, not that the pathogenic line lost its pathogenicity.

It seems clear that physiologic forms or monosporidial lines differ in general cultural characters, including rate of growth, direction of growth, type of growth, surface characters of colonies, and color. They differ also, to a certain extent, morphologically, physiologically, in tendency to mutate, and in sex and pathogenicity. Differing, as mutants do, in these characters, it follows that the factors for the characters are subject to mutation. It seemed desirable, therefore, to ascertain somewhat more precisely than was possible from general observations the environmental conditions under which mutations occur most frequently.

FACTORS AFFECTING MUTATION

There was abundant evidence from numerous experiments and observations that environment exerts a profound influence on the phenotypic characters of *U. zeae*. There was no evidence of slow, cumulative, heritable changes. Lines did not gradually lose their color, virulence, or similar characters; neither did they gradually acquire any new capabilities as a result of growing under different conditions. When changes did occur, they occurred suddenly and presumably by mutation; but there was abundant observational evidence that environmental factors affected the frequency of mutation. Therefore, experiments were made for the purpose of obtaining data along this line.

Nutrients[5]

Christensen (13), Brown (8), and others have shown that the amount and kind of culture medium may affect the frequency of mutation. As general observations indicated that this was true also of *U. zeae*, experiments were made on the effect of nutrients. In one series seven monosporidial lines were grown on six different agar media. The results are given in Table XX. There were indications that the kind of medium affects the frequency of mutation; therefore more detailed experiments were made.

TABLE XX

THE NUMBER OF MUTANTS THAT DEVELOPED IN SEVEN MONOSPORIDIAL LINES OF *Ustilago zeae* ON SIX DIFFERENT AGAR MEDIA IN TRIPLICATE FLASKS FOR EACH MEDIUM

Lines	Medium and number of mutants*						
	I	II	III	IV	V	VI	Totals
Texas A	0	0	0	0	0	0	0
Minn. A	6	8	3	8	1	0	26
Minn. G	2	0	0	0	0	0	2
Hungary A	..	..	..	0	0	0	0
Spain A	..	..	..	2	4	0	6
W. Va. A8	..	..	..	5	3	12	20
Minn. E	4	0	0	1	0	0	5
Totals	12	8	3	16	8	12	59

* Triplicate flasks were used throughout except for those listed in Column III in which duplicate flasks were used.

Media used:

I. 3.5 per cent Difco potato-dextrose agar
II. 4 per cent Difco potato-dextrose agar plus 2 per cent sucrose
III. 4 per cent Difco potato-dextrose agar plus 0.5 per cent glycerin and trace of gentian-violet
IV. 1.2 per cent Difco potato-dextrose agar plus 1 per cent litmus
V. Half-strength Shive's solution plus 3 per cent dextrose plus 1.2 per cent agar
VI. Half-strength Shive's solution plus 3 per cent lactose plus 1.2 per cent agar.

The following lines of *U. zeae* were used: W. Va. A8-5-1, Texas A, Canada A, and Minn. A. These lines were grown first on an agar medium containing various sugars without any mineral salts. The cultures attained considerable diameter but were always colorless and effuse, scarcely half the thickness of ordinary writing paper. Increasing the concentration of sugars did not stimulate more normal growth. Neither was there much difference in the growth on dextrose, sucrose, or a combination of both. No mutants appeared on the plain sugar agars. The addition of small amounts of $MgSO_4$ resulted in the production of more normal colonies, altho they were still colorless, and no mutants appeared. The addition of small amounts, .006 per cent, of calcium nitrate or sodium nitrate, however, produced a profound effect. The colonies grew faster, became larger, and were much thicker than those grown on agar containing sugars only. In addition, numerous sectors were formed when the nitrate salts were added to the medium. Increasing the percentage of nitrate salts did not result in greater frequency of mutation but seemed to have the opposite effect. For example, the medium containing .012 per cent calcium nitrate appeared to inhibit growth as well as mutation. (See Table XXI.)

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[5] These experiments were repeated by M. B. Moore and J. M. Walter while the bulletin was in press. The results in general agreed closely with those recorded here.

TABLE XXI

THE NUMBER OF MUTANTS THAT APPEARED IN FOUR MONOSPORIDIAL LINES OF *Ustilago zeae* ON VARIOUS NUTRIENT MEDIA

Medium	Sectors					Notes
	W. Va. A8-5-1	Texas A	Canada A	Minn. A	Total	
Agar 1.5%	0	1	0	0	1	
Sucrose 1.5%, agar 1.8%	0	0	0	0	0	
Sucrose 3%, agar 1.8%	0	0	0	0	0	Growth effuse. Culture of considerable diameter but very thin. Almost colorless
Dextrose 3%, agar 1.8%	0	0	0	0	0	
Sucrose 1%, dextrose 1%, agar 1.8%	0	0	0	0	0	
Peptone 1.5%, dextrose 1.5%, agar 1.8%	0	0	3	2	5	
Peptone 3%, agar 1.8%	0	0	0	0	0	
Sucrose 1.5%, agar 1.8%, $MgSO_4$ .018%	0	0	0	0	0	Slightly healthier growth than those on sugar alone
Sucrose 3%, agar 1.8%, $NaNO_3$ .006%	5	1	0	4	10	Growth more rapid. Colonies longer and several times thicker than those on sugar media
Sucrose 3%, agar 1.8%, $NaNO_2$ .006%	0	3	16	17	36	
Sucrose 1.5%, agar 1.8%, Ca $(NO_3)_2$ .012%	0	0	5	3	8	
Sucrose 3%, agar 1.8%, $(NH_4)_3PO_4$ .012%	0	0	0	0	0	Colonies only about half as large as those on nitrate media but much thicker; yellowish to orange
Sucrose 3%, agar 1.8%, $(NH_4)_3PO_4$ .012%	0	0	0	0	0	
Sucrose 1.5%, agar 1.5%, $(NH_4)_3PO_4$ .006%	0	0	0	0	0	
Sucrose 1.5%, agar 1.5% K_2HPO_4 .01%	0	0	0	0	0	Very similar to those grown on sugar media
Sucrose 1.5%, agar 1.5%, Ca $(NO_3)_2$ .005%, $(NH_4)_3PO_4$ .005%	0	0	0	0	0	Colonies slightly larger than those on nitrate media
Half-strength Shive's solution, agar 1.5%	0	6	0	2	8	
Carter's medium*	0	0	0	0	0	

* Carter's medium; 20 gm. dextrose; 10 gm. peptone; 10 gm. NH_4NO_3; 5 gm. KNO_3; 2.5 gm. K_2HPO_4; 2.5 gm. $MgSO_4$; 0.1 gm. $CaCl_2$; 20 gm. agar; 1000 cc. dist. H_2O.

No mutants appeared on sucrose agar plus different amounts of ammonium phosphate. The diameter of the colonies on such media was only about half that of those on the nitrate media, altho they were much thicker, some of them being 5 mm. or more in thickness. Color production was very pronounced, the colonies being yellowish to orange. Transfers were made from these thick, bright-colored colonies to sugar agars and the same type of growth resulted as had appeared originally, indicating clearly that there had been merely a temporary modification. Sectors were never seen on the phosphate media.

Experiments then were made to ascertain whether the addition of small amounts of ammonium phosphate to the media on which sectors were produced abundantly would inhibit their formation. To the medium consisting of 1.5 per cent agar, 1.5 sucrose, and .006 per cent calcium nitrate was added .006 per cent of ammonium phosphate. The colonies that developed were almost identical in appearance with those grown on the sugar media plus ammonium phosphate alone, altho they were slightly thicker and somewhat larger. No sectors appeared, the addition of the ammonium phosphate apparently having counteracted completely the effect of the nitrate in stimulating mutation.

It was suspected that the PO_4 radicle was responsible for the type of growth which developed when $(NH_4)_3PO_4$ was added to the media. To ascertain whether this was true, potassium phosphate was substituted for ammonium phosphate. The colonies grown on this medium differed greatly from those produced when the ammonium salt was used. The colonies were almost colorless and very effuse, resembling those produced on the sugar media. No sector formation was noted. This suggested that the PO_4 radicle was not responsible for the type of growth that developed when $(NH_4)_3PO_4$ was used as a constituent of the medium.

Temperature

From general observations and experiments there was evidence that certain lines of *U. zeae* mutated much more at certain temperatures than at others. This also is true of *Helminthosporium sativum* (14). Experiments therefore were made to determine the effect of temperature. W. Va. A8-5-1, Texas A, Canada A, and 17 Minn. A were used, with the results as summarized in Table XXII. Four separate experiments were made. In the first one the four lines of smut were grown in 4 flasks each at 8, 15, 20, 26, and 31° C. Sectors appeared only at 26° and 31° C. In the subsequent experiments tests were not made at 8° C. because the fungus failed to grow appreciably at that temperature. The results were consistent in all four tests, so it seems fairly certain that, in the lines tried, mutations either occur or become observable only at the higher temperatures. This is apparent from the summaries given in Table XXII. There were no sectors in colonies grown at 8° and 15°, only one in all those grown at 20°; eight at 26°, and eighteen at 31° C.

TABLE XXII

Effect of Temperature on the Development of Mutants in Four Monosporidial Lines of *Ustilago zeae*, Grown on Four Different Media, in Quadruplicate Flasks for Each Medium

		Forms used and number of mutants produced by each*				
Medium	Temperature, degrees C.	W. Va. A-8-5-1	Texas A	Canada A	Minn. A	Total
	8	0	0	0	0	0
	15	0	0	0	0	0
Sucrose 10 gms., malt ext. 5 cc., agar 9 gms.	20	0	0	0	0	0
	26	0	0	1	0	1
	31	0	0	1	3	4
		—	—	—	—	—
		0	0	2	3	5
	15	0	0	0	0	0
Sucrose 10 gms., malt ext. 5 cc., agar 9 gms.	20	0	0	0	1	1
	26	0	0	0	1	1
	31	1	1	5	0	7
		—	—	—	—	—
		1	1	5	2	9
	15	..	0	0	0	0
Sucrose 10 gms., $Ca(NO_3)_2$ .006%, agar 9 gms.	26	..	0	2	0	2
	31	..	0	3	0	3
			—	—	—	—
			0	5	0	5
	15	..	0	0	0	0
Shive's solution agar	26	..	4	0	0	4
	31	..	4	0	0	4
			—	—	—	—
			8	0	0	8

Light

Fairly extensive tests to determine the effect of light on the frequency of mutation were made with the same smut lines that were used in studies on the effect of temperature, but the results were inconclusive. Half of the cultures were kept in constant light and half in constant darkness, but very few sectors developed, probably because the cultures were kept at 20° C., which seems too low to stimulate mutation.

DEGREE OF CONSTANCY OF MUTANT CHARACTERS

The same monosporidial lines may vary tremendously under different environmental conditions. As a matter of fact, virtually every cultural character by which lines are recognized is subject to extremes of variation. This is true of size of colony, type of growth, consistency, elevation, topography, zonation, and marginal characters. Even under conditions which permit fairly extensive growth, the variability may be so great that one easily could conclude, on the basis of cultural characters on solid media, that the same line actually was several different lines. Some of the lines are more variable than others, but all are subject to considerable variability. As it often would be quite impossible to recognize the same line grown under different conditions, it is very important that standardized conditions be used to make comparisons of cultures grown at different times.

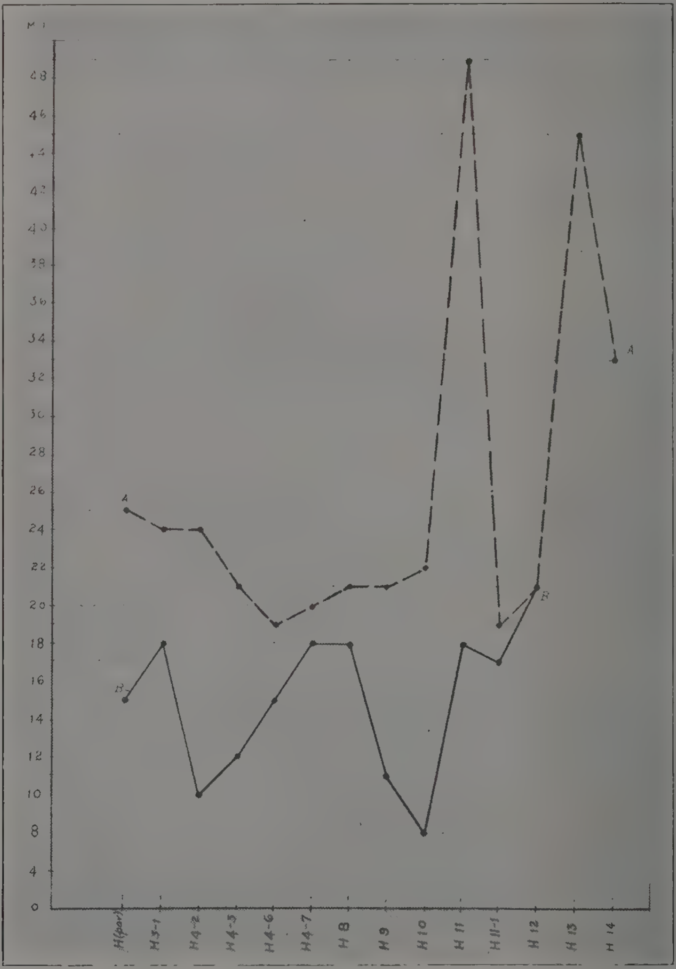

Fig. 7. Differences in the rate of radial growth of mutants and their parent, Minn. A (designated by H in diagram), when grown on two different media: *A*, potato-dextrose agar (measurements made on the 11th day); *B*, potato-dextrose agar + trace of gentian-violet (measurements on 33d day).

The composition of the medium may have a profound influence on the appearance of colonies. The amount of moisture, very slight differences in the composition and the amount of medium used, may affect the appearance of colonies considerably. The effect of media is shown clearly in Plate VIII, which shows Minn. A3-1-2 on three different media. It will be noted that the surface on potato-dextrose agar is decidedly convoluted but there are radial ridges near the margin, with fine white mycelium at the edge. On potato agar the growth is much more effuse; therefore the convolutions are less distinct, and the marginal ridges almost imperceptible. On 1 per cent glycerine potato agar there are a few convolutions near the center of the colony and deep radial furrows with only a faint suggestion of radial ridges on a few of the lobes near the edge of the colony.

Several series of lines from W. Va. A8 were grown at various times under uniform conditions on potato-dextrose agar, potato-dextrose plus half-strength Shive's solution agar, and litmus-lactose agar. A close study was made of the characters of W. Va. A8-4 to A8-4-5, inclusive, and of A8-5 to A8-5-5, inclusive. In all cases it was possible to distinguish the different lines on any one of the media alone, but the characters of the same line on the three media were quite different. The colonies on litmus-lactose agar, for example, were on the average considerably larger than those on the other two media, but the growth was more effuse. There was a tendency for most characters to appear most sharply defined on the potato-dextrose plus Shive's solution agar. The characteristic color was generally most distinctive; the characteristic topography of the surface was most clearly defined; and the marginal characters were usually more outstanding. In some of the lines there was a tendency toward the production of a black color. This was always deepest on the agar containing Shive's solution. In lines characterized by rugose, contoured, or reticulate topography, the most pronounced development occurred on this medium. The reticulations were always larger and coarser and the radial ridges were almost always more sharply defined. These characters were almost entirely suppressed on litmus-lactose agar, altho in some cases there were indications of their occurrence. It is noteworthy, however, that when colonies grown on one medium were transferred again to another medium, they then assumed the distinctive characters of the particular line on that particular medium, indicating that there was no gradual fixing of characters because of growth on a particular kind of medium.

Effect of temperature on the appearance of colonies is shown fairly well in Plate IX, which pictures colonies of four lines grown at 26° C. and 18° C. (10° for A8-5-2-1). It will be noticed that colonies of W. Va. A8-5-2-1 resemble each other at the two temperatures, but the margin is more nearly entire at 26° C. At 10° C. it is quite irregular and decidedly raised. The most characteristic difference is the fact that at 10° C. there is a tendency for part of the colony to grow away from the medium, forming a cup-shaped structure near the center. At 26° there are two well-defined zones in the colonies of A8-5-4, a central mound which is only slightly contoured, and a marginal band lighter in color and characterized by the presence of mid-sized, branched radial folds which intertwine somewhat at the base. At 18° C. there is virtually no zonation and the radial ridges are considerably suppressed, altho there are a few radial furrows. The colony of A8-5-7-1 at 26° is flat, smooth, and distinctly zonate. On the other hand, at 18° it is convex to umbonate, verrucose to rugose, and not zoned. It will be noted that the topography of the two colonies of A8-5-1-3-3 tends to be approximately the same, altho it is more pronounced at the higher temperature. The shallow radial folds produced near the margin of the colony at the higher temperature are entirely absent at the lower temperature. Furthermore, the surface of the colony at 26° C. was somewhat waxy, while at the lower temperature it was fine and felt-like. In most cases the colonies were smaller at 18° than at 26°, altho in at least one instance they were equally large at both temperatures.

Despite the fact that there is great phenotypic variability in the same lines of *U. zeae*, it is remarkable that they seem to be so constant for given conditions, except for mutation. There has been no evidence whatever, in the authors' studies, that a permanent change is induced by environmental conditions, except in so far as they stimulate mutation.

The concept of the "educability" of fungi apparently still is held by some mycologists. Loss of virulence of cultures, loss of factors for color production, and loss of sporulating ability have repeatedly been explained on the basis of degradation resulting from artificial culture. In *U. zeae*, the only changes of this nature that the authors have detected were clearly explicable on the basis of mutation, not on the basis of degeneration because of saprophytic nutrition. Mutability could easily account for much of the so-called educability, as pure lines of a very mutable fungus are difficult to maintain. One could scarcely guarantee the homogeneity of a culture which had been grown in culture for several months or a year without precautions to avoid transferring mutants along with the parent. The authors have observed hundreds of times that small, indistinct mutants may be very numerous on agar slants. It would be relatively easy to transfer these mutants during routine transfers. Furthermore, as pointed out previously, mutants may appear as indistinct sectors or patches on the colony. What assurance could there possibly be that dozens of these mutants were not transferred unless precautions were taken to avoid it?

It seems to the authors that the best method of insuring the purity of cultures of a mutable fungus is to grow it in flasks containing a medium on which mutation does not occur commonly. Even then precautions must be taken to transfer from the parent colony and not from the parent colony plus one or more of the mutants. Brown (8) has called attention to the danger of transferring mutants and permitting them to accumulate in routine cultures unless similar precautions are taken. If stock cultures are carried in test tubes, it is desirable to grow them on a relatively poor medium for mutation and transfer frequently. Even then there is no assurance, in the case of a fungus like *U. zeae*, that the population of the cultures will remain homogeneous.

From all experiments and observations made by the authors they can only conclude that *U. zeae* is extremely unstable genetically, but not in the sense imputed by such words as educability, adaptation, and Abkultur. They have repeatedly, in fact thousands of times, observed the appearance of new lines, but only by mutation and hybridization.

It has been claimed that the phenomenon of reversion tends to prove that so-called mutants are not in reality true mutants. In *U. zeae* reversions to the parental type do occur, but in a relatively small percentage of cases; and then the evidence is that they occur by mutation.

Despite the frequency of mutation, the authors have grown many lines in culture for periods of time ranging from a few months to three years, without observing any inexplicable change. In fact, some of the cultures, principally those that mutate only very infrequently, have been grown constantly on artificial media for four years without alteration of their essential characters. The following experience is illustrative of this fact. During the summer of 1928 one of the authors made comparative studies of W. Va. A8-5-1 to W. Va. A8-5-5, inclusive. His final notes on some of these mutant lines were taken on July 4, 1928, and on the others, September 10, 1928. He then gave the cultures to one of the other authors for experiments on physiologic characters and did not see them again until September 1, 1929. Then he recognized the numbers in a temperature series and looked up his original notes to see how the descriptions corresponded with the characters apparent at that time.

One line, W. Va. A8-3-1, arose in a slightly pinkish colony of A8-3 as a large fan-shaped sector which was characterized by conspicuous radial folds and an olivaceous color, both of which were entirely lacking in the parent colony. The mutant was grown on several different media for comparison with the parent. The outstanding characters of the mutant on potato-dextrose agar at that time were its rather coarse growth, the distant and pronounced radial folds, and a mouse-gray to olivaceous color, obscured somewhat by a whitish-powdery superficial growth, and a mycelial margin of medium texture. On September 1, the colonies on potato-dextrose-maltose agar grown at 26° C. were as nearly identical in appearance with those grown on a slightly different medium, at room temperature, a year previously as could be determined from the author's notes and memory. On inquiry it was found that this particular line had been transferred at least twenty times during the year; had been subjected to varying conditions of nutrition and temperature; and had produced at least one mutant. Nevertheless it was virtually identical in appearance a year later. Stock cultures of the mutants were then compared with stock cultures of the parent and it was obvious that the characteristic folds of the mutant were quite apparent and would serve to distinguish it readily from the parent, even on fairly old agar slants.

Another of the cultures in this series was W. Va. A8-5-1. On potato-dextrose agar, September 10, 1928, the size of the colonies was recorded as 50 mm., and the outstanding characters were described as follows: "Most of the colony distinctly convoluted, with a border about 1 cm. wide in which there are distinct radial ridges rather unique in the fact that they are shaped like a tuning fork; color of the central area of the colony grayish, the remainder gray-buff, and the marginal area a clear buff orange." It so happened that the colonies on potato-dextrose-maltose agar on September 1, 1929, were exactly 50 mm. in diameter, the central area was grayish, the remainder gray buff; the radial ridges were precisely as had been described a year previously; and the color of the marginal area in which they occurred was again a clear orange buff. W. Va. A8-5-4 was described September 10, 1928, as having a decided central mound 20 mm. in diameter and grayish buff with a tinge of purple in color on potato-dextrose agar, delicate pink on potato-dextrose plus Shive's solution agar, with a broad margin of rather fine, radial lines or ridges. On September 1, 1929, the central mound and the marginal characters were as described a year previously, altho the color was somewhat deeper. Furthermore, a note was made on September 10, 1928, that the color of A8-5-4 on potato-dextrose plus Shive's solution agar was deeper orange than that of A8-5-1. Precisely the same observation was made on September 1, 1929.

The characters mentioned above appear to be due to genetic factors, as they tend to appear under conditions that are in the least favorable for the growth of the organism. They can be altered or suppressed temporarily but always tend to reappear when the organism is grown under fairly normal conditions. The above are merely a few observations which convince the authors that the mutant lines are different genotypically and not merely phenotypically. It may be objected that the differences between mutants and their parents may be due to changes in the cytoplasm rather than in the nucleus, that they are, therefore, somatic rather than genotypic changes. It is true that thus far the criterion of heritability has been satisfied only for asexually propagated mutants. It has been pointed out, however, that mutants often differ from parents in sex factors. This surely would seem to involve a change within the nucleus. Furthermore, there is evidence that factors for mutant characters are inherited through sexual reproduction as well as asexual propagation.

A study of the f_1 lines from crosses between lines of *U. zeae* indicates that there are multiple factors for most of the characters discussed in the foregoing pages, and that the organism is highly heterozygous for most characters. This complicates breeding tests.

It seems clear, however, from Table XXIII that the change in type of growth of at least one mutant from that of the parent is genotypic. The f_1 lines[6] from Minn. A x Minn. F, both mycelial types, were mostly mycelial. But those from Minn. F x Minn. A13, a sporidial mutant from Minn. A, were mostly sporidial. That Minn. A12 and Minn. A13, sister mutants from Minn. A, carry different genetic factors for growth type is indicated by the fact that most of the f_1 lines from Minn. A12 x Minn. D were predominantly mycelial. From Minn. A13 x Minn. D, on the other hand, there were 14 mycelial, 7 intermediate, and 11 sporidial types. This furnishes evidence that Minn. A13 differs from its parent, Minn. A, and from its sister mutant A12, in genetic factors for growth type. The change, therefore, would seem to be genotypic in nature—true mutation.

TABLE XXIII

GROWTH TYPE OF f_1 LINES FROM CROSSES BETWEEN CERTAIN LINES OF *Ustilago zeae*

Cross and growth type of parents	Number of f_1 lines of different growth types		
	Mycelial	Intermediate	Sporidial
Minn. A (mycel.) x Minn. F (mycel.)	13	0	1
Minn. A13 (sporid.) x Minn. F (mycel.)	4	2	7
Minn. A13 (sporid.) x Minn. D (mycel.)	14	7	11
Minn. A12 (mycel.) x Minn. D (mycel.)	12	0	1

DOES TRUE MUTATION OCCUR IN USTILAGO ZEAE?

The authors have used the term mutation to designate the phenomenon resulting in the sudden and fortuitous origin of the new lines of *Ustilago zeae* discussed in the foregoing pages. Some microbiologists and geneticists may, and probably will, object to the use of the term in this connection. Possibly we have not proved mutation.

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[6] The sporidia on the promycelia of chlamydospores resulting from a cross can be considered the gametes of the F_1 individuals. They are therefore designated f_1, and cultures resulting from single sporidia are designated f_1 lines.

Whether we have depends largely on the concept of what mutation really is. The word has been used rather loosely, perhaps, in the literature of microbiology. The authors have used it to denote the sudden appearance of new lines of *U. zeae*, which apparently are not the result of normal segregation nor of abnormal environmental conditions, and the mechanism of whose origin is not, and possibly cannot be, known. Possibly the authors have used the term in a too liberal sense; that depends, of course, on one's opinion of what the word should connote.

There probably is no universal agreement, even among geneticists, as to the precise meaning of the word mutation. Baur (2, p. 339) defines it as follows: "Erbliche Verschiedenheiten zwischen den Eltern und ihren Nachkommen—auch den vegetativ entstandenen—welche nicht auf Bastardspaltung beruhen, sondern welche andere Ursachen haben." If this definition is accepted, the authors think they have proved the case beyond reasonable doubt for *U. zeae*. The changes that occur certainly persist through many asexual generations and evidently also through sexual fusions. They apparently are not the result of hybrid segregation, altho the authors can furnish no guarantee that there is not an unsuspected, or at least undetected, segregation of factors after sporidia have been formed on the promycelium, where segregation of sex factors and of those for cultural characters certainly usually occur. It is just such uncertainty as this that probably provoked Brierley's expressions of agnosticism in his philosophical essays on mutation in micro-organisms and in the interpretation of his own results (5, 6, 7).

Brierley (7) maintains that the phenomenon described as mutation in micro-organisms cannot be equated with mutation in higher plants and animals. His opinion is that it is premature to use the term in mycological studies when there is evidence only of changes of unknown genetic causation. Because of the ignorance of genetic constitution and chromosomal relations in fungi, Brierley thinks there can be no assurance of genetic purity even in monosporous lines. He points out that a monosporous line may be heterozygous and therefore has no greater genetic value "than a single-seed or a single-tuber culture derived from a probably or possibly cross-bred higher plant of unknown genetic constitution" (7, p. 724). He states further that no geneticist would accept such material as a sound basis for experimental work unless by breeding experiments he could analyze its genetic constitution and obtain progeny homozygous for the character he wished to investigate. This has not yet been possible for fungi. Attention is called also to the fact that monosporous fungal lines may be heterokaryotic, hence genetically impure, as a result of sexual fusions or anastamosing of vegetative hyphae. The chance assortment of nuclei in cell division might then result in the appearance of "new strains." Brierley does not deny the possibility of mutation in fungi but states definitely that he is of the opinion that no single case has been described which satisfies the criteria essential to proof.

It is unfortunate that words must be used to describe phenomena and express concepts, because few words can be used with mathematical precision. If a scientific term meant precisely the same thing to all investigators, there undoubtedly would be fewer arguments—and probably less literature to read. After all, what most likely is needed is accurate descriptions of phenomena and clear-cut distinctions between those that are different. In the present case the difficulty seems to be that we do not know sufficiently well, at least in microbiology, just what the mechanisms are by which so-called mutations are brought about. The word mutation often has been used to designate sudden and unexplained changes of more or less permanent nature in the observable characters of micro-organisms. Blakeslee (3, 4), La Rue (35), Christensen (13), Leonian (36), Christensen and Stakman (15), and Stakman, Christensen, and Hanna (45) used the word mutation more or less in this sense. Stevens (46), Brown (8), Chaudhuri (12), Mitter (39), and others use the word saltation, while Burgeff (10), Caldis and Coons (11), and others use the term variants. Still others speak of modifications or "Dauermodifikationen." Caldis and Coons, for example, are of the opinion that the "achromatic variations" which they studied in several different fungi "represent semi-permanent variations which are different from the parent form somatically rather than genetically. These are the dauer-modifications of Jollos ——————." It would seem to be a pertinent question whether mycologists have used these different terms to describe essentially identical phenomena or whether the phenomena described under the various terms really were different. It is beyond the province of this bulletin, however, to subject to critical scrutiny all of the literature dealing with the so-called mutations in fungi.

That variations occur in fungi is a fact that even the most sceptically minded probably will accept as a platitude. But what is the nature of these variations? Ramsbottom (41), Brown (8, 9), Christensen (13), and many others have pointed out that environmental factors may profoundly affect the appearance of a fungus. As Ramsbottom (41, p. 40) expresses it, "Further investigations, such as those of Matruchot thirty years ago, showed that when certain media were used a fungus might have its facies so altered that by a systematist it would be placed in another genus. It is now one of the best known features of culture work that the form of a fungus can be altered in all sorts of ways by the use of different media." With this statement most mycologists will agree heartily and most of them probably will agree that these purely temporary variations or modifications are not inherited even through vegetative propagation. Fungi may be shocked into looking queer by subjecting them to extraordinary stimuli, but they ordinarily regain their composure very soon after the stimuli have been removed. These ordinary, non-heritable variations certainly do not explain what have been called mutations. Possibly these statements would be so generally accepted as to be superfluous. But there still are some students of fungi who apparently believe in "educability"—the transmission of characters acquired as a result of environmental influences.

If fungi are "educable," many of them are very refractory subjects. At least that is the judgment of the two authors of this bulletin who have tried long and arduously to make fungi appreciate the benefits of education. We do not deny that cultures may be so weakened by maltreatment that their recuperative powers are taxed somewhat, but the pathogenic fungi to which we have tried to give opportunities for leading a different life have refused to do so. We can only conclude that the potentialities of fungi, like those of higher organisms, are determined by their genes, and the only way in which their potentialities can be changed is by changing their genes. Which means that fungi are the product of the interaction of genetic and environmental factors, just as higher organisms are, and that when heritable changes occur they come about as the result of hybridization or mutation. Possibly "Dauermodifikationen" may occur, as they apparently do in protozoa, but the authors do not believe they are dealing with this type of phenomenon in *U. zeae*, altho Goldschmidt (22) seems to be of the opinion that the preponderance of evidence indicates that "mutations" which he observed in *U. violacea* were of the nature of "Dauermodifikationen."

Jollos (29) described "Dauermodifikationen" in Paramecium. He was able to induce tolerance for arsenic by growing non-tolerant lines of Paramecium in a medium containing it. This acquired ability persisted through many asexual generations, but was lost immediately following conjugation and was eventually lost also in vegetatively propagated lines after they had been grown for some time on arsenic-free media. More persistent "Dauermodifikationen" were induced by calcium salts, inasmuch as the modification, reduction in rate of division, persisted not only through many asexual generations (about nine months in some cases), but also through two successive conjugations. One line, for example, reverted to normal after the second conjugation, but required several months longer for reversion when propagated asexually. Jollos considers this a case of "Dauermodifikation" also, as he does not believe the germ plasm was changed. His concept of this phenomenon seems to be that a line can adapt itself temporarily to certain environmental conditions and retain its acquired ability for some time after the removal of the stimulus that brought it about. Reversion, loss of the acquired characters, is gradual as long as the organism propagates asexually, but it is either immediate or relatively rapid when sexual reproduction intervenes.

Jollos describes also what he considers a true mutation. He obtained a line of Paramecium comprising individuals that were characteristically smaller and more tolerant of high temperatures than the parental line. The new line retained its characteristics for more than a year in normal culture and also after repeated conjugations. Jollos therefore considers that it is justifiable to consider this a case of true mutation, a genotypic change. He thinks there are three categories of variations: ordinary modifications, "Dauermodifikationen," and mutations. Granting the correctness of his conclusions, the question arises as to whether the same type of phenomenon which he describes as "Dauermodifikation" occurs in fungi, and whether the so-called saltations or mutations fall into this category.

Baur (2, pp. 61-62) suggests that the adaption of many bacteria to particular animal or plant hosts and the specialization of certain rust fungi for certain hosts may possibly be of the nature of "Dauermodifikationen." The authors are firmly of the opinion that this is not true for the rust fungi, as one of them has devoted many years to a study of the question and is forced to conclude that physiologic forms of rust fungi are remarkably constant, as long as they are propagated asexually.[7] Uredinial lines of *Puccinia graminis*, Pers., on which most of the studies have been made, are dikaryophytes and may be heterozygous, but there is no evidence of segregation or chance assortment of nuclei; and cultures derived from a single urediniospore are dikaryotic clones with certain infective capacities that do not become permanently modified as a result of host influences. On the other hand, there is very strong evidence that the physiologic forms arise by mutation and hybridization, altho mutations apparently occur much less frequently than in many other fungi.

The conjugate nuclei in the dikaryophase of *Puccinia graminis* may have different factors for pathogenicity and sex; and the pathogenic capabilities of a uredinial line or physiologic form may be the component of the factors in the two nuclei, that probably were derived from two haploid lines. In this respect the aecial and uredinial stages of the rust would correspond with the dikaryophase of *U. zeae* and other smut fungi—with the difference that in the smuts the haplonts can propagate independently and the dikaryophytes do not reproduce as such, while in the rusts the haplonts cannot multiply independently, and the dikaryophytes can and do propagate independently. The physiologic forms or parasitic strains of *P. graminis,* therefore, are clones which owe their parasitic peculiarities to two conjugate nuclei containing different genes, but all the evidence obtained by the senior author and his associates supports the view that the forms differ genotypically and not merely phenotypically. These forms may be, and often probably are, heterozygous and many types of segregates may result after sexual fusion, but that is precisely what is expected. The teliospores are the true diplonts and one may expect the same sort of segregation on a teliospore promycelium as on a promycelium of a chlamydospore of *U. zeae.* The authors cannot believe that the forms are at all comparable with "Dauermodifikationen," and they are of the opinion that anyone who examines the published evidence or makes the experiments will agree.

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[7] For a brief summary of the evidence and references to the original papers see No. 43 in the bibliography.

Brown (8) was unable to obtain evidence of slow cumulative change in *Fusarium.* The saltations which he described appeared sporadically, suddenly, and without any apparent cause. They did appear in greater numbers on certain media than on others, but Brown offers a perfectly logical explanation for that. The same thing was true of the mutants described by the authors for *U. zeae.* And why should not mutations in fungi occur more frequently under some conditions than others? The mass of data on mutations induced in higher organisms by X-rays and radioactive substances should furnish sufficient supporting evidence, if it were needed, that mutation occurs more often under some conditions than others. But there is a decided difference between the gradual and temporary acquisition of a "purposeful" character, as in the case of Jollos' "Dauermodifikationen," and the sudden appearance of new lines that may or may not be better adapted to the conditions under which they were produced.

Caldis and Coons state that nutrients, light and darkness, and reaction of substratum were not controlling factors leading to production of the fungal variants they studied. Nevertheless they reach the following conclusions (11, p. 215). "It is the opinion of the writers that the variants dealt with in this paper represent rather semi-permanent variations which are different from the parent form somatically rather than genetically. These are the 'dauer-modifications' of Jollos (29), which perhaps by drying of the mycelium and lack of nutritional connection with the substratum, have become changed from the normal. With respect to certain attributes they may be looked upon as attenuated forms. Instead of being new species they are rather to be looked upon as cultures lacking certain physiological powers. They resemble, in some respects, the Abkulturs of Fusaria and the so-called attenuated cultures of bacteria and fungi. They may have arisen from cells whose protoplasm has been poisoned, or perhaps affected by some unknown biological factor, and which are tardy in recuperation until supplied with the necessary conditions. This study illustrates that the criteria established for proof of the educability of fungi are necessary and that what may seem plausible evidence of the establishment of new forms in pure cultures needs careful and protracted investigation." This may be the correct explanation for the phenomena observed by Caldis and Coons, but it does not seem probable that it would explain some of the new entities of *Mucor genevensis* described as mutations by Blakeslee (3), nor the variants of *Phycomyces nitens* described by Burgeff (10). Blakeslee describes a "dwarf mutant" that lost the power to produce sporangia, to produce zygospores hermaphroditically, and did not unite sexually with plus and minus races of dioecious species. This mutant remained constant from 1913 until 1920, when Blakeslee published his statement regarding it. Some of Blakeslee's mutants reverted to the parental type and might be considered by some, therefore, as "Dauermodifikationen." But the suggested explanation for reversion given by Burgeff (10) for *Phycomyces nitens* and by Blakeslee for his Mucors seems more reasonable. Burgeff considers that mutation affects only some of the nuclei in *Phycomyces*, which is multinucleate. He calls these variants mixochimeras, in which the more rapid division of normal nuclei would account for reversions. Blakeslee thinks that his reverting mutants also may be mixochimeras.

What we have called mutations in *U. zeae* conceivably might be due to one of the following: (1) ordinary variation or modification; (2) "Dauermodifikation"; (3) mutation; (4) the isolation of individual lines from a mixed population; (5) the chance assortment of nuclei in the budding of possibly heterokaryotic sporidia; (6) ordinary segregation; (7) extraordinary segregation. That they are not ordinary modifications is perfectly clear from the fact that the characters of the new lines are long persistent. The authors do not believe that their mutations are analogous to Jollos' "Dauermodifikationen," because there is no gradual fixing of certain characters as a result of certain stimuli, followed by loss of the characters when the stimuli are removed. The new lines arise suddenly, sporadically, frequently in some lines, seldom in others. The new characters are persistent but may or may not enable the organism better to adjust itself to certain conditions. Very often factors for rate of growth, color, sex, pathogenicity, etc., seem to be lost, but in other cases there seems to be a gain. Possibly the authors are using "Dauermodifikation" in a too narrow sense, but, as they understand it, the essence of the concept is that it is a modification induced by definite environmental stimulus, that the modification persists for a limited time after the stimulus is removed and then is gradually lost if the organism multiplies asexually, and suddenly lost in sexual reproduction. The change is presumed to be in the cytoplasm, and possibly to a lesser extent in the nucleus. In the case of *U. zeae* the change often is in the nucleus, as the new lines may be quite different from their parents in sexual powers. Neither the cause of the change nor the nature of the change in *U. zeae* seems analogous to that which Jollos observed in Paramecium.

If it will be agreed that the preponderance of evidence is against the probability that the new lines of *U. zeae* are either ordinary modifications or "Dauermodifikationen," there remain the possibilities that they are merely lines isolated from a mixed population, or that they are segregates. As the changes occur in great numbers in monosporidial lines, the possibility of isolation from an originally mixed population is ruled out. Before considering the other two possibilities it may be well to review what is known about the nuclear phenomena in *U. zeae*.

The chlamydospore nucleus typically is the result of karyogamy. It is a fusion nucleus, and is therefore diploid. On germination the spore produces a promycelium, and the diploid nucleus undergoes division. A second division occurs, resulting in the formation of four nuclei which become distributed in the promycelium. Usually three septa are then laid down, resulting in the formation of a four-celled promycelium, each cell of which contains one nucleus. Four sporidia then form, one on each cell of the promycelium. During this process the nucleus in the promycelial cell again divides, one daughter nucleus going into the sporidium and one remaining in the promycelial cell, which can, therefore, produce successive crops of sporidia. The sporidia are typically uninucleate. It has been shown by Hanna (24) that two of the sporidia usually are of one sex and two of another, altho sometimes they may belong to four sexual groups. Furthermore, the individual sporidia on the promycelium may produce colonies of different color and type of growth; hence there has been segregation of factors for sex, for color, and for type of growth, in one or both of the nuclear divisions in the promycelium. That is, reduction division has occurred. The sporidia, then, are haplonts, potential gametes; and monosporidial lines are haploid or gametic clones, as in most other Ustilaginaceae (34). That this probably is true is indicated by the fact that a number of times the authors have isolated several sporidia from monosporidial lines and compared them in respect to cultural characters and sex. The resulting lines behaved alike.

If monosporidial lines are in reality gametic clones it would be justifiable to consider the variant sectors that arise in colonies of these clones as true mutations, provided they result from a genotypic change. The authors think they do, as the general cultural and physiological characters are constant—except as they may again change suddenly, presumably as a result of mutation. And, what is more important, the changes evidently affect the nucleus—the germ plasm, as is indicated by changes in sexuality. There is evidence, also presented in this paper, that at least some mutant characters, type of growth for example, persist through the sexual stage. Therefore it would seem that the criteria for mutation have been satisfied reasonably well. The authors freely admit that nothing is known about chromosomal behavior, if indeed definitely organized chromosomes exist; hence the evidence for reduction division in the promycelium is necessarily circumstantial. Possibly there is segregation of some kind in the process of budding of sporidia in sporidial cultures or in cell division in mycelial cultures, but, if there is, it would seem to be unusual, as only a very few individual sporidia or mycelial cells in proportion to the enormous number in a colony differ from the rest. The authors admit, also, the possibility of heterokaryosis, altho the sporidia appear to be characteristically uninucleate and to arise from uninucleate cells of the promycelium.[8] An explanation of the appearance of sectors on this basis would appear to be rather far-fetched in a fungus like *U. zeae* with its rather definite alternation of haploid, dikaryo, and diploid phases. The possible validity of such an explanation for the appearance of so-called mutants would seem to be greater in the case of fungi whose cells are typically multinucleate. If the so-called mutations in *U. zeae* are not due to gene changes or chromosomal aberrations, it seems more probable that they are due to some sort of unknown segregation.

The authors consider the evidence good, however, that changes, heritable both through asexual propagation and sexual reproduction, occur in gametic clones of *U. zeae;* that the changes are not due to segregation; and therefore are mutations.

SIGNIFICANCE OF MUTATION

Ustilago zeae comprises an indefinite number of haploid lines differing from each other in many characters. There seems to be no good reason why these lines should not be considered physiologic forms, as some of the most conspicuous differences between them involve physiologic characters. The authors are not disposed to urge the acceptance of this viewpoint, however; possibly it is just as well to use the term "line." Most of these lines are unisexual; hence hybridization is prerequisite to normal infection, except occasionally, as shown in Part II.

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[8] Since the manuscript was written M. B. Moore and J. M. Walter have made an extensive study of the nuclear condition in several monosporidial lines. The sporidia and hyphal cells were almost universally uninucleate. The very few sporidia in which there were two nuclei were budding or about to bud. The senior author studied the slides thoroly and is convinced that the sporidia and hyphal cells in the lines studied are definitely uninucleate.

As the unisexual lines are very numerous and differ in many characters, large numbers of new genotypes may result from hybridization. Add to this the fact that mutation is so common, and it is not surprising that there are so many lines.

U. zeae seems to be extraordinarily variable and mutable. Most of the other smut fungi investigated seem to be far less mutable. Despite the enormous amount of work done with *U. violacea,* very few mutations have been recorded for this species. And, in extensive experiments with *U. tritici, U. nuda, U. hordei, U. levis,* and *U. avenae,* Rodenhiser (42) observed mutation only in *U. hordei* and *U. avenae,* and rather rarely in them.

The extreme variability and mutability of *U. zeae* is interesting in itself and emphasizes the statements of Leonian (36) and Brown (9) regarding the caution necessary in creating taxonomic systems of fungi that vary and mutate extensively. It seems probable that some of the peculiar behavior attributed to fungi in culture, loss of virulence for example, may often be due to mutation, or, if one prefers a more noncommittal statement, to the production of variants or saltants. Mutation seems also to be significant in the broader aspects of the problem of pathogenicity in *U. zeae.*

The fact that some mutants are adapted to growing well at a wide range of temperature suggests one way in which mutation may be important in epidemiology. Those lines that tolerate wide extremes of temperature are likely to be most prevalent. Under certain conditions they may develop well, while those lines with more rigidly fixed temperature requirements may develop very poorly or not at all. Temperature, then, may determine the prevalence of certain lines in different regions or in the same region in certain seasons.

Mutation may result in the development of lines with different physiologic and sex factors, and there is strong evidence that the lines differ in pathogenicity. The corn smut pathogene, therefore, comprises a large number of parasitic strains. The possible implications of this fact in the control of the disease by immunization are quite obvious. Christensen and Stakman (15) already have called attention to this fact. Much more work must be done to determine the pathogenic capabilities of combinations of mutant lines of *U. zeae* and of the nature of resistance in corn before final conclusions can be drawn. We know, however, that there are numerous parasitic strains, that new ones are being produced by mutation and hybridization, and that these facts may have important practical implications, but how important must be determined by future investigations.

SUMMARY

1. *Ustilago zeae* comprises an indefinite number of monosporidial or haploid lines that differ from each other in so many physiologic characters other than sex that they might well be considered physiologic forms.

2. Numerous sectors arise in cultures of most monosporidial lines of *U. zeae*. "Patch mutants" also may occur, but less frequently than sectors.

3. Some lines mutate abundantly, while others seem to do so rarely. From one line the authors isolated, within a year, 220 mutants, 162 of which were different. From another line 70 were obtained. A few lines have never been observed to mutate; others have been grown in culture for long periods of time without mutating; then they suddenly began to mutate.

4. Mutants may differ from their parents in type of growth, consistency of colonies, direction of growth, size of colonies, elevation, color, and surface characters of colonies.

5. Mutation often affects physiologic characters. Some of the outstanding physiologic differences between mutants were: ability to liquefy gelatin, digestion of casein, reduction of nitrates and iodine, and rate of growth at different temperatures.

6. The morphology of sporidia of different mutant lines may be different.

7. Pathogenicity and sex are closely interrelated in *U. zeae*. The pathogene seems to be predominantly heterothallic, the fusion of lines of opposite sex usually being prerequisite to infection. Therefore, the pathogenicity of combinations of lines only can be studied in most cases, altho it is shown in Part II of this bulletin that some monosporidial lines can cause infection alone.

8. It is not known to what extent pathogenicity is a function of sex factors and to what extent of physiologic factors. That it is not a function of sex only is indicated by the fact that certain lines may unite to form chlamydospores without producing large galls, while others may produce large galls.

9. Mutations in sex occur. Some mutants seem to have lost completely the sex factors that enable their parents to unite with other lines.

10. Many mutants seem to have lost factors for pathogenicity while others seem to be more virulent than the immediate parent.

11. Nutrients and temperature appear to affect the rate of mutation. In a series of experiments on the effect of nutrients, no mutants were observed on sugar media nor on sugar media plus $MgSO_4$ or phosphates. One appeared on plain water agar, a few on peptone-dextrose agar, and a considerable number on sugar media plus nitrates.

The largest number of mutants appeared in cultures grown at fairly high temperatures.

12. There seems to be good evidence that what the authors have designated mutations are in fact true mutations. The variant sectors or patches arise in monosporidial lines, which appear to be haploid clones; the new characters persist through asexual propagation, and there is evidence that at least some of them persist through sexual fusions. The change, therefore, appears to be genotypic.

13. The results with *U. zeae* suggest that some of the remarkable variability attributed to fungi in culture, loss of virulence, change in sex, and loss of sporulating ability, for example, often may be due to unobserved mutations.

14. Mutation would seem to be very important in the corn smut problem, especially in epidemiology and breeding for smut resistance.

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PLATES

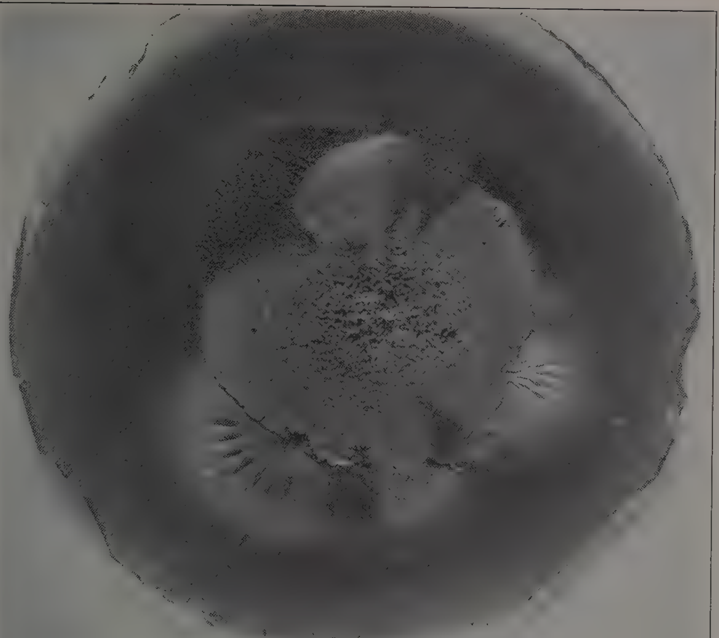
PLATE I

How Mutants Arise

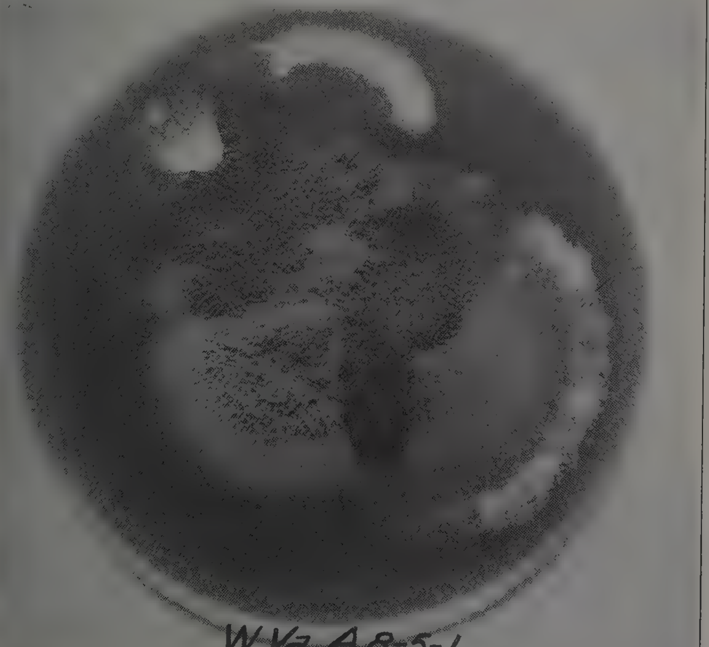
A. Minn. A, a monosporidial line on potato-dextrose-malt agar. Mutants mostly appearing as wedge-shaped or fan-shaped sectors. One patch mutant near the upper left of the colony. Note difference in size, color, and type of growth of the different mutants. It is noteworthy that some of the mutants are much darker in color than the parent colony, while others are much lighter.

B. W. Va. A8-5-1, a mutant derived from W. Va. A8, on potato-dextrose agar. In addition to the varied assortment of fan-shaped mutants, there are patch mutants near the center of the colony.

PLATE I



Minn. A



W. Va. A 8-5-1

PLATE II

Cultural Differences between Mutants and Their Parent

Minn. A and seven of its mutant lines on potato-dextrose-sucrose-malt agar. Note the range in color, topography, and marginal characters among the mutants. Some of the mutants are decidedly darker in color than the parent. Note also the counter-clockwise growth near the margin of Minn. A7.

PLATE II

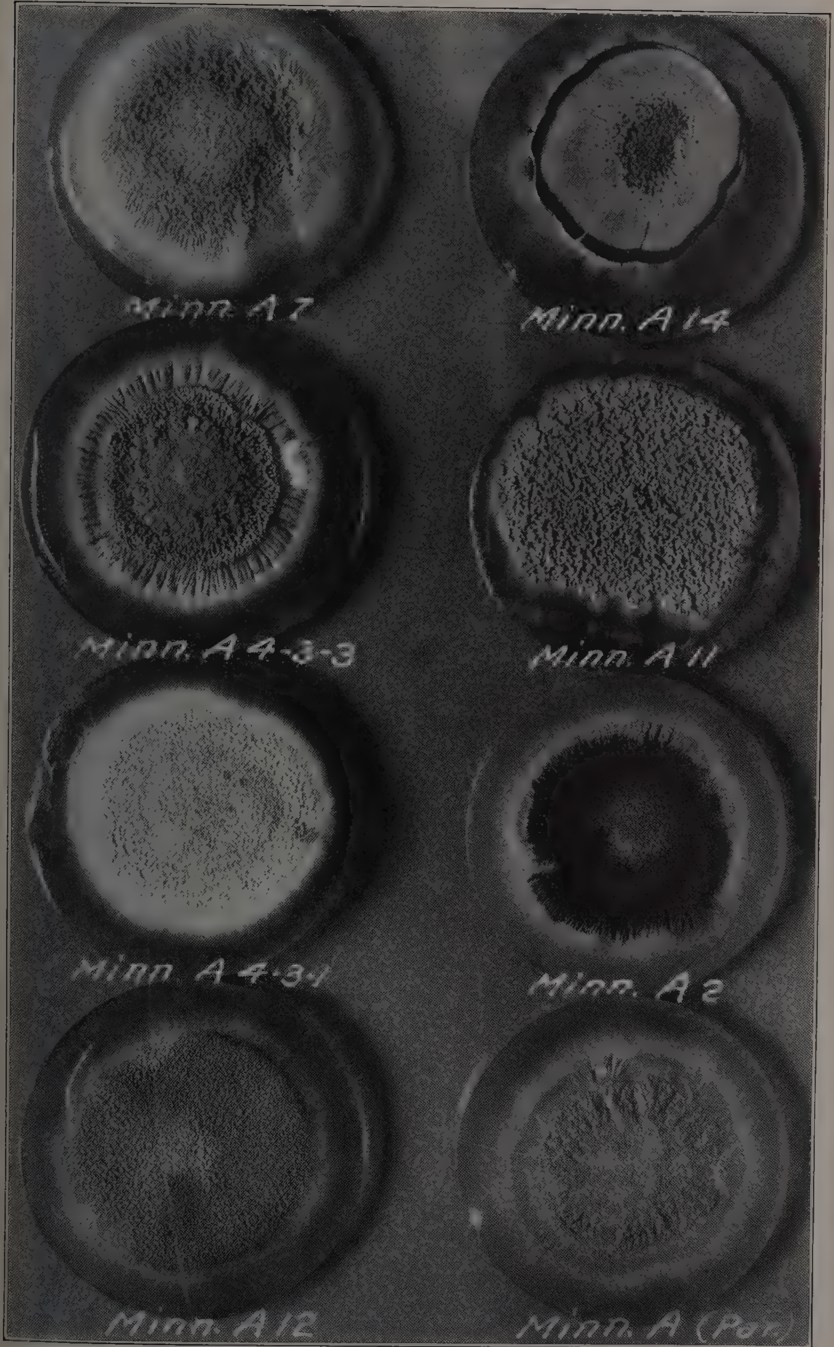

Minn. A 7
Minn. A 14
Minn. A 4-3-3
Minn. A 11
Minn. A 4-3-4
Minn. A 2
Minn. A 12
Minn. A (Par)

PLATE III

Cultural differences between three mutants from Minn. A on potato-dextrose-sucrose agar. Note counter-clockwise direction of growth in A3-1-1-1. The differences between these three mutants are typical of those between the 70 mutant derivatives obtained from Minn. A.

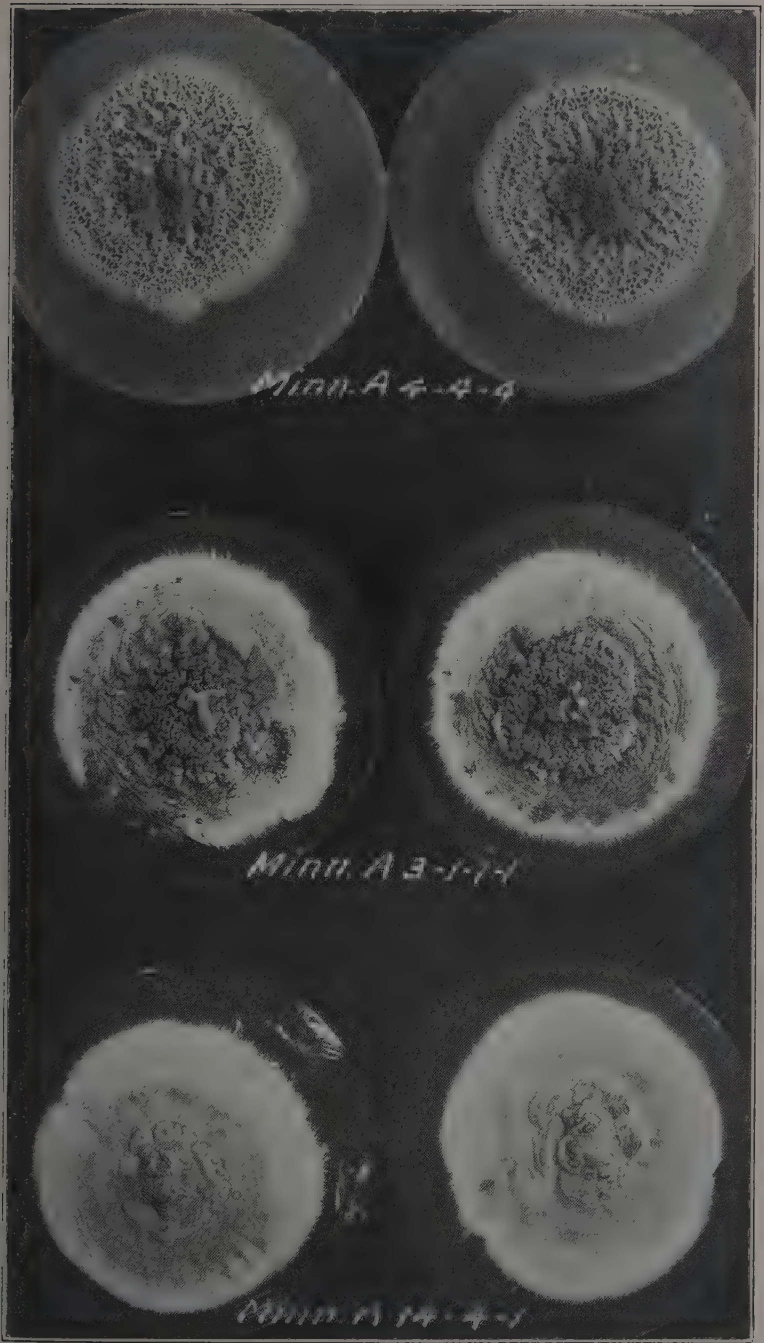

Minn. A 4-4-4
Minn. A 3-1-14
Minn. A 14-4-1

PLATE IV

Eight mutants derived from W. Va. A8, grown under uniform conditions. Note the range of color, topography, zonation, and type of growth. All of the mutants had appeared a year or more previous to the time the photograph was taken, and had retained their distinctive characters on many kinds of media and under many different sets of environmental conditions. Note the decided differences between mutant lines of A8-5, which produced so large a number of the mutants whose origin is shown in Figure 1.

PLATE IV

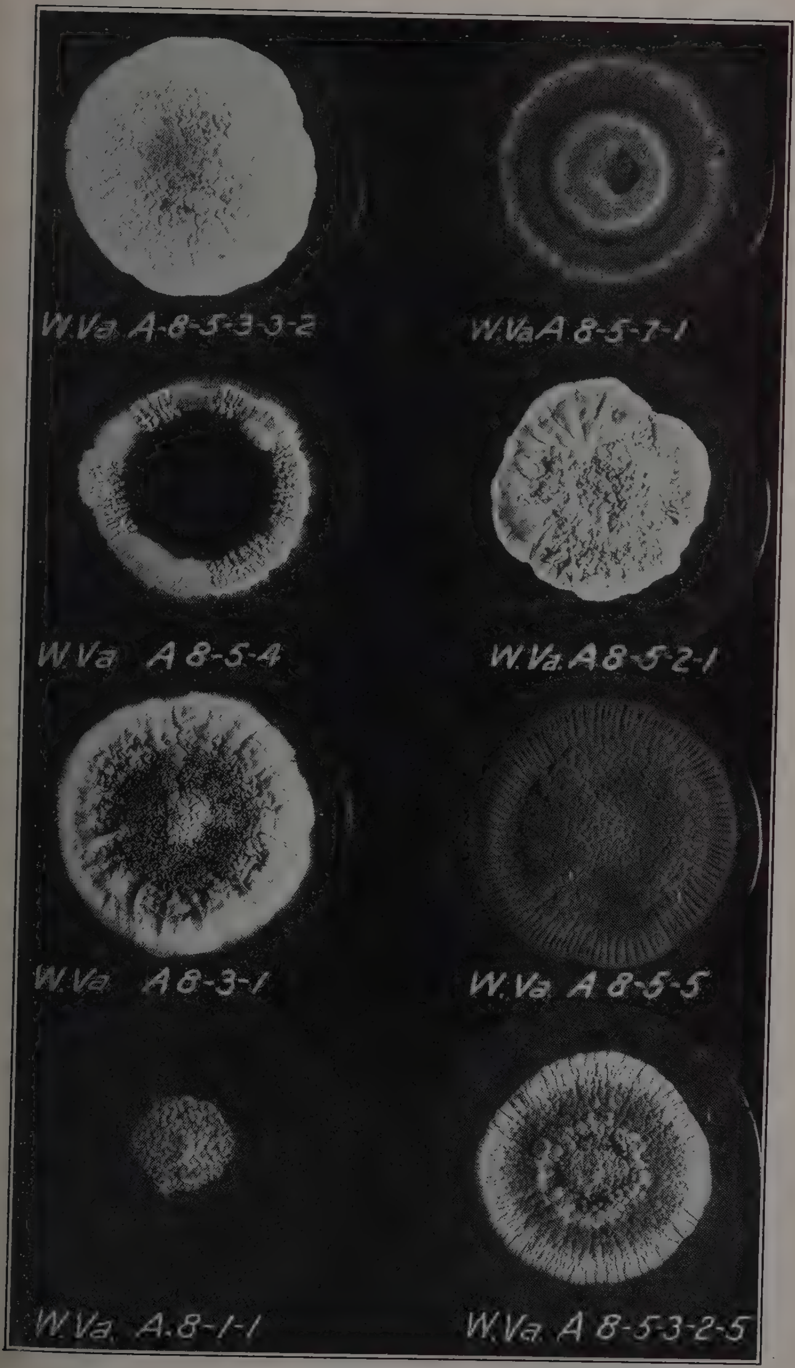

W.Va A-8-5-3-3-2
W.Va A 8-5-7-1
W.Va A 8-5-4
W.Va. A 8-5-2-1
W.Va A 8-3-1
W.Va A 8-5-5
W.Va. A.8-1-1
W.Va. A 8-5-3-2-5

PLATE V

The differential ability of mutant lines of W. Va. A8 to digest casein, as indicated by clear zone around colonies growing on milk agar. Relative amount of digestion indicated by white area. The photograph was taken through the bottom of the flask; therefore the white medium looks dark in the photograph and the cleared area appears white.

PLATE V

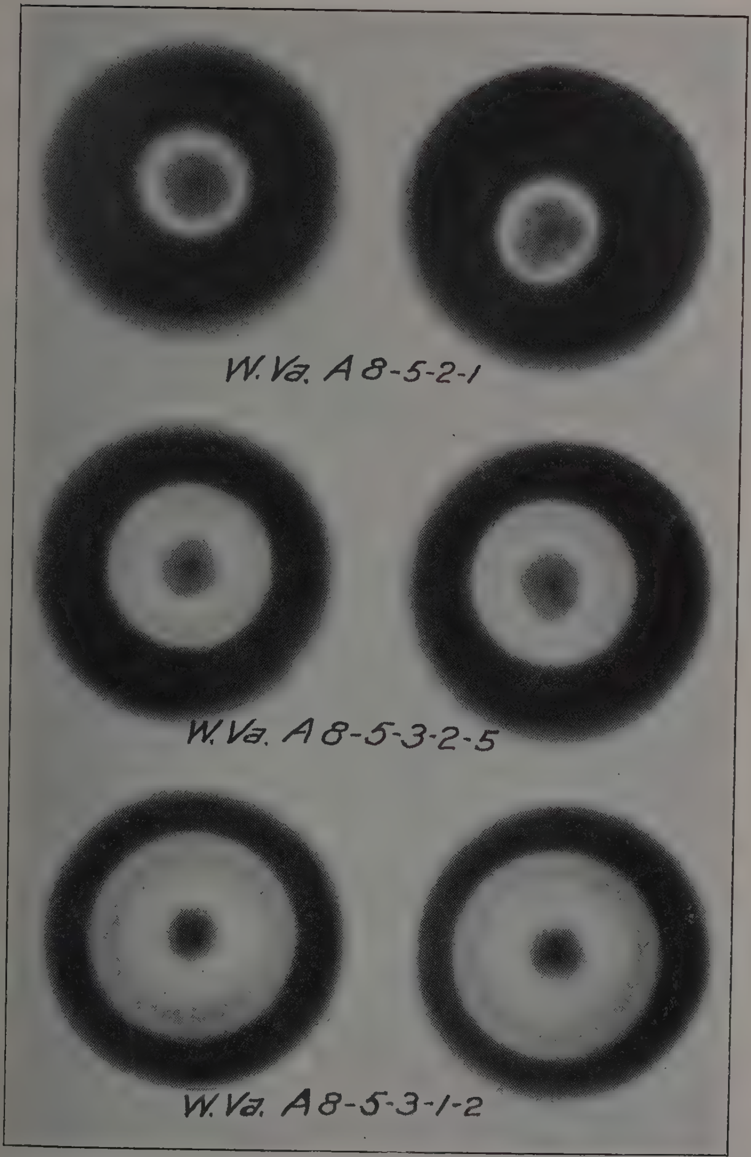


PLATE VI

Mutants W. Va. A8-3-1, A8-1-1, and A8-5-3-1-2, photographed 24 hours after adding iodine to medium containing KNO_3. Iodine added 13 days after inoculation. It is evident that mutants differ decidedly in rate of action on iodine, indicating that they differ greatly in physiologic characters.

PLATE VI

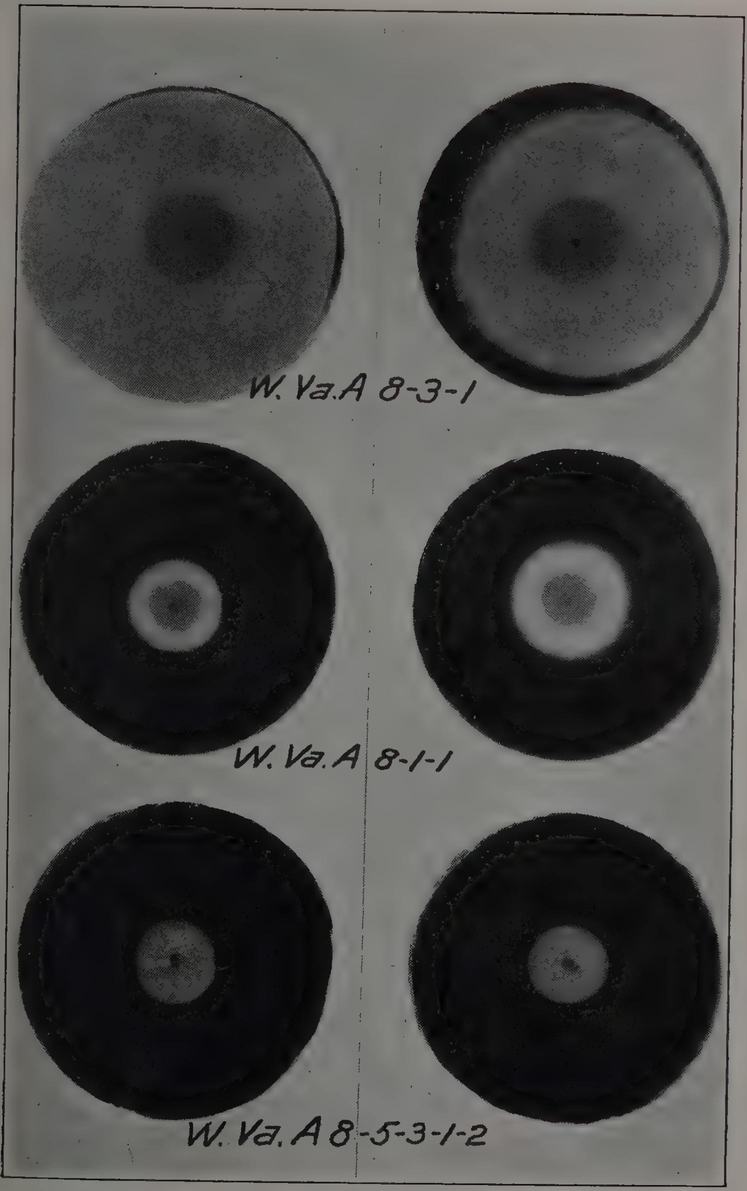


PLATE VII

Effect of Temperature on Rate of Growth of Different Mutant Lines

Note the difference in ability of lines to grow at the extremes. A8-5-2-1 grows fairly well at 10° and 34° C., whereas A8-5-4 grows scarcely at all at the extremes, and A8-3-1 is intermediate between the two.

PLATE VII

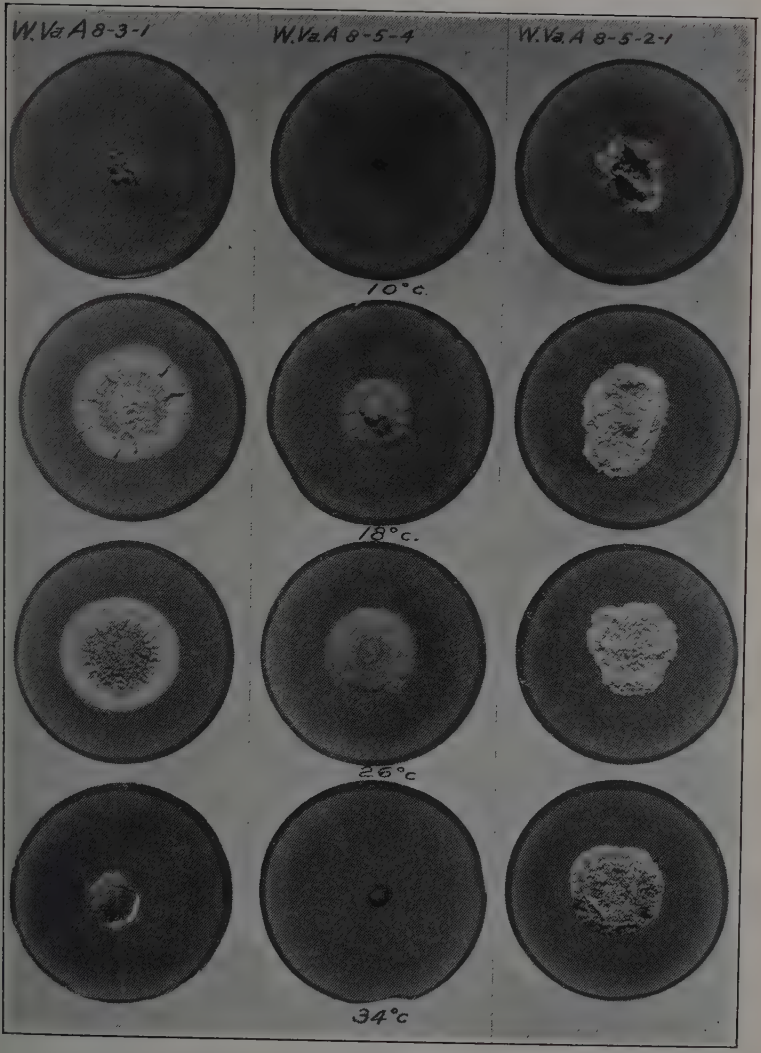


PLATE VIII

Effect of Medium on the Appearance of Colonies of a Single Mutant Line,
Minn. A3-1-2

P. A. = potato-extract agar; P. D. A. = potato-extract agar + 3 per cent dextrose; P. A. + 1 per cent glycerine = potato-extract agar + 1 per cent glycerine.

While the appearance of the colonies on the different media is entirely different, it is evident that certain characters tend to remain constant. Certain points of resemblance are apparent on close examination of the colonies, especially those on potato-glycerine agar and potato agar. In general, there are wide variations in the appearance of a single monosporidial line grown on different media.

PLATE VIII

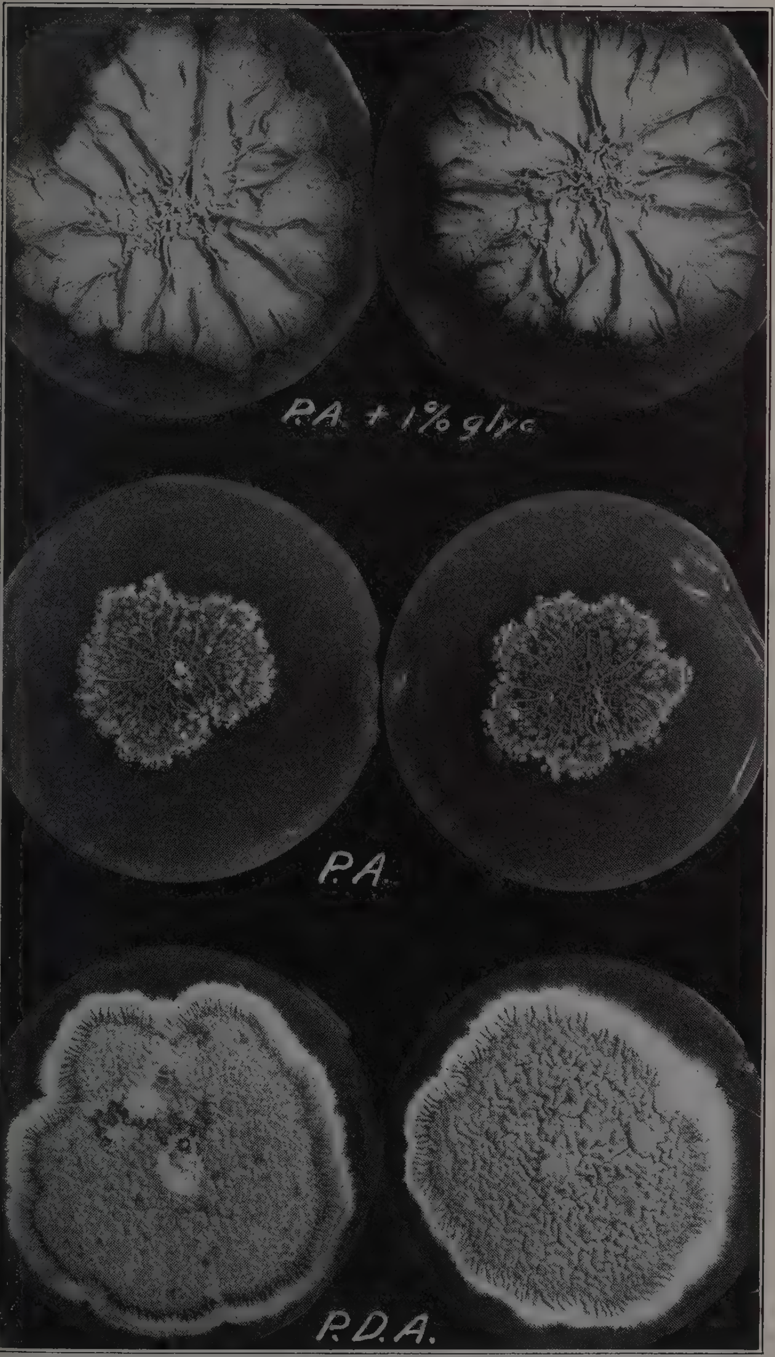


PLATE IX

Effect of Temperature on the Appearance of Colonies of Mutant Lines

Four mutant lines of W. Va. A8 grown at 18° and 26° C. The mutant in upper left-hand corner was photographed at 10° C. in order to show more clearly the cuplike structure in the center, but unfortunately the photograph did not bring it out.

Note the absence of zonation in W. Va. A8-5-4 at 18° C., also the difference in color from that of the colony grown at 26°. Note also the difference in topography and zonation of the two colonies of W. Va. A8-5-7-1 at the two temperatures.

PLATE IX

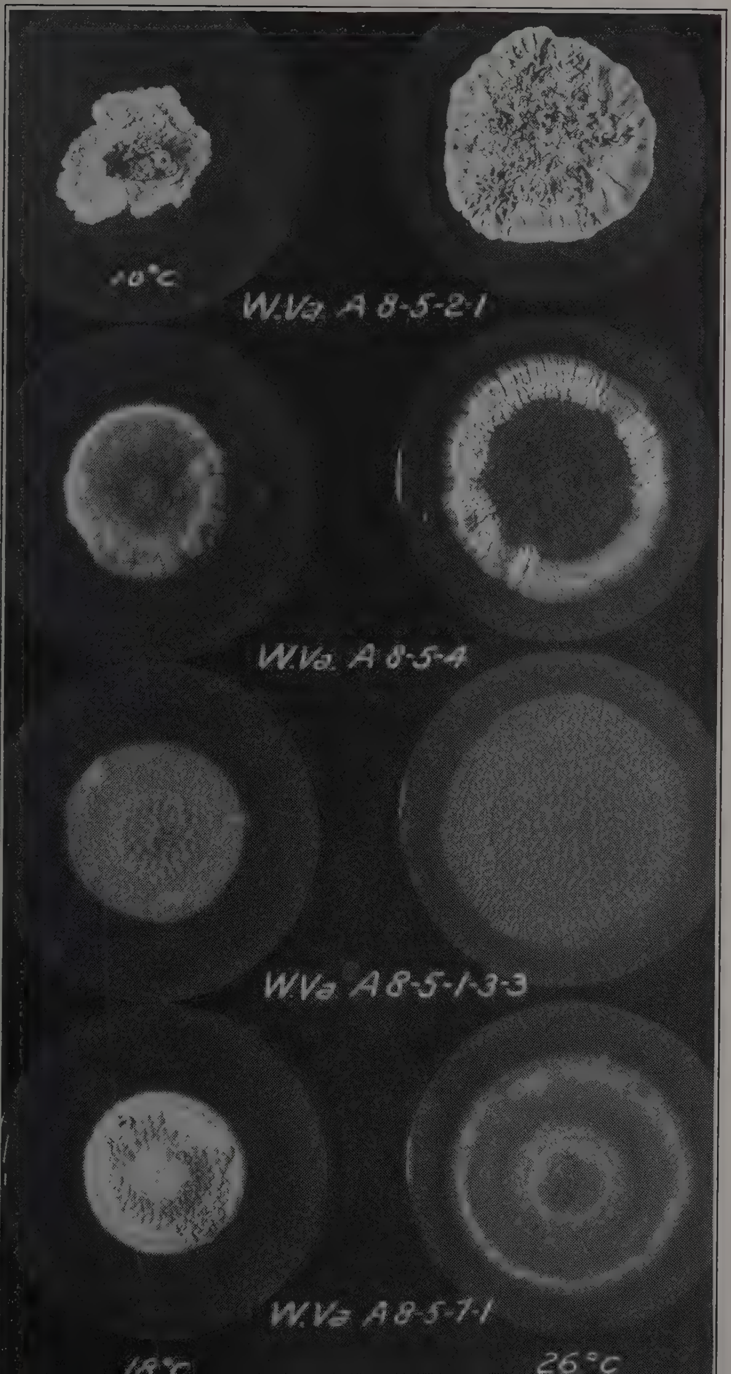
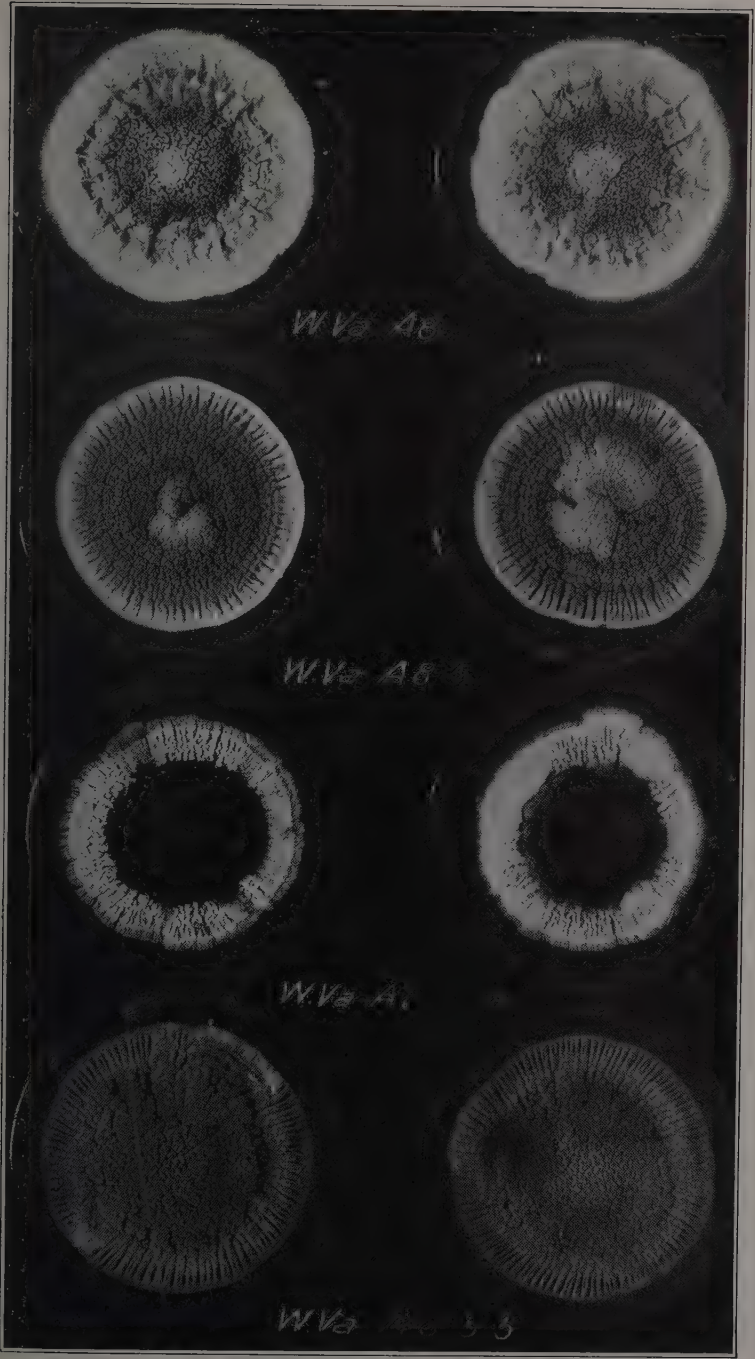


PLATE X

Persistence of Cultural Characters

Duplicate colonies of four mutant lines of W. Va. A8 showing cultural characters that have persisted since the lines were isolated; the radial folds and color zones of A8-3-1; the characteristic topography and radial furrows near the margin of A8-5-1; the decided topographic and color zones of A8-5-4. Note the similarity of A8-5-1 and A8-5-5, but note also the slight but distinct differences. The permanence of cultural characters such as these is one of the facts that convince the writers that what they have called mutants are the result of genotypic changes.

PLATE X



Part II. Hybridization

J. J. Christensen[1]

INTRODUCTION

Stakman and Christensen (10), Hanna (6), and Eddins (3) have shown that *Ustilago zeae*, like most other smut fungi investigated (8, 9), is usually heterothallic. This means that the fusion of two monosporidial lines of opposite sex usually is prerequisite to normal infection and production of chlamydospores in the smut galls on corn plants. The sporidia are haplonts; they are potential gametes. Monosporidial, that is, gametic, lines propagate by budding, by growth of haploid mycelium, or by both methods—in nature and in nutrient media; hence it is possible to study the characters of gametic lines in culture. The results of such studies are reported in Part I, where it is shown that gametic lines may differ from each other in many characters other than sex and that numerous new lines arise by mutation. It is desirable to know, also, to what extent new lines arise as a result of hybridization. For this reason crosses were made between monosporidial lines and a study was made of lines derived from the sporidia produced on the promycelia of the resulting chlamydospores.

ARE THERE "GEOGRAPHIC STRAINS"?

Hanna (6) showed that promycelia of *U. zeae* might be either bisexual or quadrisexual, i.e., the 4 primary sporidia might belong to 2 or to 4 sexual groups. In this respect *U. zeae* is similar to many of the gill fungi, in which the 4 basidiospores on a basidium may belong either to 2 or to 4 sexual groups. But Kniep (7), Hanna (5), and Vandendries (11) showed that there are "geographical strains" in *Schizophyllum commune, Coprinus lagopus,* and *C. micaceus,* respectively. For example, according to Hanna (5), the basidiospores of any individual fruiting body of *C. lagopus* belong to 4 sexual groups only, and the mycelia from these 4 spores also would belong to 4 sexual groups. When, however, pairings were made between 11 mycelia derived from one wild fruiting body and 11 from another, there was complete fertility between them. In 6 fruiting bodies studied in this manner there were 24 distinct sexual groups instead of the 4 which might be expected. Kniep already had shown that, while the spores of individual fruiting bodies of *Schizophyllum commune* belong to 4 sexual groups, there was complete interfertility between different mycelia of monosporous origin derived from fruiting bodies collected at some distance from each other. Vandendries (11) obtained similar results with two wild fruiting bodies of *Panaeolus campanulatus*. He found, on the other hand (12), a high degree of intersterility between some strains of *Coprinus micaceus*.

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[1] The writer is indebted to Dr. E. C. Stakman for help in the preparation and arrangement of material.

Stakman and Christensen (10) showed in the case of *U. zeae* that normal infection might result from inoculating corn with paired lines of different sex from the same locality and also from widely separated geographic regions. For example, monosporidial lines from New Hampshire, Mississippi, and Canada produced normal galls when paired with monosporidial lines from Minnesota, and different lines from Minnesota also paired with each other. Later, Hanna (6) successfully crossed monosporidial lines from Italy with some from Minnesota, and showed that the sexual groups of the Minnesota collection apparently were identical with those of the Italian collection.

During 1928 and 1929 further experiments of this nature were made. Minn. E and Minn. F, two lines of opposite sex isolated from material collected at University Farm, St. Paul, Minnesota, were paired with 18 monosporidial lines, all culturally different, obtained from several different countries. Results are summarized in Table I. It will be seen that all of the lines paired successfully with either Minn. E. or Minn. F. There were differences in the virulence of the various combinations, but the results are not recorded here. It is evident, however, that lines from widely separated regions and those from the same region may or may not hybridize. There is no evidence either of complete interfertility or intersterility. Each line tried, regardless of its origin, united either with Minn. E or with Minn. F but not with both.

TABLE I

RESULTS OF INOCULATING GOLDEN BANTAM CORN WITH MONOSPORIDIAL LINES OF *Ustilago zeae* FROM DIFFERENT GEOGRAPHIC REGIONS IN COMBINATION WITH MINN. E AND MINN. F, TWO LINES OF OPPOSITE SEX

Lines	Lines and gall formation*	
	Minn. E	Minn. F
Colorado A	+	—
West Virginia A7	+	—
West Virginia A8	+	—
Canada A	+	—
France A	+	—
Hungary A	+	—
Italy B	+	—
Spain B	+	—
Minn. E	—	+
Minn. A	—	+
Pennsylvania A	—	+
Texas A	—	+
Texas B	—	+
West Virginia A	—	+
France B	—	+
Italy A	—	+
Italy C	—	+
Spain A	—	+

* + = gall formation; — = none.

TERMINOLOGY

Monosporidial lines of *U. zeae* are characteristically haploid. When two lines of opposite sex are grown together on artificial media their mycelia or sporidia may intermingle, but apparently do not fuse (6, 10). When, however, they are inoculated into corn plants, haploid hyphae of opposite sex fuse, the nucleus from each haploid hypha passing into the fusion cell, which then would contain two nuclei of opposite sex. These nuclei do not fuse at once but remain associated and divide conjugately, so that each cell of the resulting mycelium, the dikaryophase, is binucleate. Plasmogamy has therefore occurred, but karyogamy is delayed until the chlamydospores are formed, when the two nuclei of each spore-mother cell fuse, thus giving rise to the true diplophase. The chlamydospore nucleus is a fusion nucleus; therefore the spores are zygotes. On germination the chlamydospores produce a promycelium, the fusion nucleus divides, the two daughter nuclei in turn divide, thus resulting in the formation of four nuclei, one for each cell of the typically four-celled promycelium. A primary sporidium is then formed on each cell of the promycelium, each nucleus again divides, one from each cell passing into the sporidium, and one remaining in the promycelial cell. As reduction division occurs in the promycelium (6), the sporidia are haplonts. They are functional gametes that can propagate asexually, making it possible to study the characters of gametic lines.

When crosses are made between gametic lines of opposite sex, then, the immediate result is the dikaryophase, followed by the true diplophase, which in turn gives rise to the haploid phase. How are these phases to be interpreted genetically? Clearly the sporidia or mycelia of monosporidial lines are, at least partly, gametic in nature. Possibly in the strictest sense the gametes are the haploid nuclei, altho the sporidia may equally well be considered as gametes. But what about the dikaryophase; is it unique in the fungi, or is it approximately equivalent to part of the F_1 generation in higher plants? The answer depends on one's interpretation of the essential criteria of the diploid condition. Some mycologists consider that the dikaryophase is essentially equivalent to the diplophase because of the well-established fact that the two nuclei clearly influence the morphology, growth, and pathogenicity of the hyphae. Haploid hyphae, containing nuclei of one sex only, are usually rather fine, in the host plant, and normally cannot grow extensively in the tissues. When nuclei of opposite sex are associated in the hyphae, however, the hyphae are large, often grow vigorously, and are distinctly pathogenic. Consequently there seems to be some justification for the argument that conjugate nuclei exert approximately the same sort of effect on the hyphae as do fusion nuclei. If it is agreed that there is no essential difference between the dikaryophase and the diplophase, the first fusion cell is the zygote and the F_1 generation begins with the growth of the mycelium from that cell. The F_1 would then include the mycelium in the corn tissues, the chlamydospore, and the promycelium, where gametogenesis—the production of sporidia, or, if one prefers, of the haploid nuclei—occurs. If the essential identity of the dikaryophase and true diplophase is denied, the chlamydospores are zygotes, the F_1 is restricted to the promycelium, and the dikaryophase has no real counterpart in higher plants. In either case the sporidia are the F_1 gametes, unless the haploid nuclei, only, are considered as gametes. Cultures derived from single sporidia following a cross are designated in this paper as F_1 gametic lines (or merely as f_1 lines), for they really are gametic lines whether the entire sporidium or its nucleus, only, is considered as the true gamete. For convenience, the monosporidial lines used in making the crosses are designated parents or parental lines (p_1). In reality they are the parental gametes, but it may be permissible to refer to them as parents because it simplifies the terminology.

CROSSES MADE FOR STUDY OF f_1 LINES

The following crosses were made: Minn. A13 x Minn. F; Minn. A13 x Minn. D; Minn. A13 x Canada A; Minn. A x Canada A; Minn. A12 x Minn. D; and Minn. A x Minn. F. Minn. A, Minn. D, and Minn. F originated from material collected at University Farm, St. Paul, Minnesota, Minn. A and Minn. D having been isolated from the same promycelium. Minn. A12 and Minn. A13 are sister mutants from Minn. A. Canada A was derived from a smut gall obtained from Canada. For convenience, the sporidia were numbered in succession as they were obtained from germinating chlamydospores resulting from a given cross. Thus, Minn. D x Minn. A13.2 refers to the second sporidium isolated from cross Minn. D x Minn. A13. The crosses were made by mixing liquid cultures of the monosporidial lines and injecting the mixture into the corn plants with a hypodermic syringe. The method was essentially that described by Stakman and Christensen (10).

The sporidia were not taken directly from the promycelia. Instead, the chlamydospores were sown on agar media and, after they had germinated and produced sporidia, isolations were made from various places in order to obtain sporidia from as many different chlamydospores as possible. In all, 102 individual sporidia were isolated from the 6 crosses. The individual sporidia were first placed in Van Tieghem cells and, after they had multiplied sufficiently, transfers were made to agar slants and allowed to develop for 3 or 4 days. Transfers were then made to a series of triplicate flasks containing 30 cc. of Difco potato-dextrose agar. These cultures then were used for comparative tests. The crosses are indicated in the usual manner and the f_1 (monosporidial) lines from each cross are numbered serially. Thus, Minn. A13 x Minn. F.6 indicates the monosporidial line obtained from the sixth sporidium isolated from germinating chlamydospores resulting from the cross Minn. A13 x Minn. F. When single sporidia were isolated from a monosporidial line such as Minn. A13 x Minn. F.6, the lines were designated in the same manner. Thus, Minn. A13 x Minn. F.6.1 indicates the first monosporidial line isolated from the sixth monosporidial line from cross Minn. A13 x Minn. F.

CHARACTERS OF f_1 LINES

Sexual Characters[2]

Heretofore there has been evidence of four sex groups in *U. zeae*. Stakman and Christensen (10) found only two, while Hanna (6) found that the four sporidia on certain promycelia fell into two sexual groups, and those on others belonged to four groups. In the first case the results indicated that difference in sex was due to a single factor difference while in the second, at least two factor pairs were involved. In the present work the author made a large number of crosses in order to determine the pathogenic capabilities of different combinations of lines. As pathogenicity depends so largely on sexual reactions between different lines, an attempt was made to find out how many sexual groups there were among the F_1 gametes from crosses. The results are given in Tables II, III, and IV.

In Table II are recorded the results of pairing 13 f_1 lines from Minn. A13 x Minn. F with the parents and with 3 other monosporidial lines. There are at least 5 sexual groups among the 13 f_1 lines, on the basis of their ability to form chlamydospores when paired with other lines. Lines 5, 8, 7, and 10 appear to be identical sexually with Minn. A13, while line 2 is like Minn. F. Lines 3 and 13 did not unite with either parent, but each united with one of the testers, and lines 1, 4, 6, 9, 11, and 12 failed to unite with any of the lines with which they were mated.[3] Minn. F and A13 x F.2 both formed a virulent combination with Minn. A, but were less virulent with its mutant A13, while

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[2] The writer has used as a criterion of sex differences the ability of lines to produce chlamydospores in the host plant. If two lines do not produce chlamydospores, they are considered to be of the same sex. It is conceivable, of course, that such lines may produce dikaryophytes which cannot grow in the corn tissues because of the absence of necessary factors for pathogenicity. There is strong evidence, however, including microscopic studies, indicating that this is not true.

[3] It was found subsequently that lines 1 and 6 both united with line 9, but 1 and 6 did not unite; hence 1 and 6 appear to belong to one sexual group and 9 to another. In the discussion of Table II, however, conclusions are based only on data available when the table was prepared.

A13 x F.3 united readily with A, but not at all with A13. It will be noted also that lines 5 and 8, like A13, produced only light infection with Minn. F, but 7 and 10 caused heavy infection with this line. It is a question whether the differences in degree of infection are due to sex factors or to distinct factors for pathogenicity. If they are due to the former, there are six sexual groups instead of five, but, for reasons given later, the author has used as a criterion of sex differences only the ability to form chlamydospores, altho recognizing the possibility that degree of infection also may be an indication of them.

TABLE II

RESULTS OF INOCULATING GOLDEN BANTAM AND MINN. 13 CORN IN THE GREENHOUSE WITH f_1 LINES FROM MINN. A13 x MINN. F. IN COMBINATION WITH THE PARENTS AND WITH MINN. A, MINN. B, AND MINN. D.

Parents and f_1 lines	Lines and infection					Lines and degree of infection*				
	A	A13	F	B	D	A	A13	F	B	D
A13	—	—	+	+	+	—	—	L	H	H
A13 x F.5	—	—	+	+	+	—	—	L	H	H
do 8	—	—	+	+	+	—	—	L	H	H
do 7	—	—	+	+	+	—	—	H	H	H
do 10	—	—	+	+	+	—	—	H	H	H
F	+	+	—	—	—	H	L	—	—	—
A13 x F.2	+	+	—	—	—	H	L	—	—	—
do 3	+	—	—	—	—	H	—	—	—	—
do 13	—	—	—	—	+	—	—	—	—	VL
do 1	—	—	—	—	—	—	—	—	—	—
do 4	—	—	—	—	—	—	—	—	—	—
do 6	—	—	—	—	—	—	—	—	—	—
do 9	—	—	—	—	—	—	—	—	—	—
do 11	—	—	—	—	—	—	—	—	—	—
do 12	—	—	—	—	—	—	—	—	—	—

* + = infection; — = no infection; H = heavy infection; L = light infection; VL = very light infection.

Table III summarizes the results of pairing thirteen f_1 lines from Minn. A12 x Minn. D with the parents and, to some extent, with each other. To the right of the table the lines are grouped according to their sexual reactions with the parents. Lines 4, 8, 10, and 13 are like A12 in that they combine with D and not with A12; lines 5, 6, 9, and 12 are like D, as they combine with A12 but not with D; and 1, 2, 3, 7, and 11 fail to combine with either parent. With respect to their reactions with the two parents, therefore, there appear to be only three sexual groups. But an examination of the complete table shows that there are at least nine groups. Only 8 and 13 are like A12, and 5 only is like D. Lines 1, 2, 3, 7, and 11 appear identical when mated with the parents only, but, on the basis of their reactions with other lines, it is clear that they are different, with the possible exception of 3, which was dropped from consideration because it was mated with the parents only. There apparently are at least nine sexual groups on the basis of the pairings that were made. In addition to those lines that appear to be identical with the parents, 4 and 10 seem to be alike, and 6 and 9 are alike on the basis of the matings made. Line 12 is like 6, but not like 9, which is assumed to be identical with 6. Whichever combination is assumed, the total number of groups is not changed. All possible combinations were not made; had they been, it is possible that still more sexual groups could have been demonstrated.

TABLE III

Results of Inoculating Golden Bantam and Minn. 13 Corn with f_1 Lines from Minn. A12 x Minn. D with the Parents and with Each Other

Lines		Lines and infection*																		
				A12 x D.																
		A12	D	1	2	3	4	5	6	7	8	9	10	11	12	13	Group		A12†	D
Parents	A12	o	+	—	—	—	—	+	+	—	—	+	—	—	+	—	1	A12	—	+
	D	+	—	—	—	—	+	—	—	—	+	—	+	—	—	+	2	4	—	+
A12xD.	1	—	—	o	—	o	—	—	—	+	o	—	o	—	o	o	3	8	—	+
	2	—	—	—	o	o	+	—	—	—	o	—	+	+	o	o	4	10	—	+
	3	—	—	o	o	o	o	o	o	o	o	o	o	o	o	o	..	13	—	+
	4	—	+	—	+	o	o	+	o	—	—	+	—	—	—	o	5	D	+	—
	5	+	—	—	—	o	+	o	o	—	+	—	+	—	—	o	2	5	+	—
	6	+	—	—	—	o	o	o	o	o	o	—	o	+	o	o	6	6	+	—
	7	—	—	+	—	o	—	—	o	o	o	—	o	o	—	o	7	9	+	—
	8	—	+	o	o	o	—	+	o	o	o	+	o	—	+	o	1	12	+	—
	9	+	—	—	—	o	+	—	—	—	+	—	+	+	—	+	6	1	—	—
	10	—	+	o	+	o	—	+	o	o	o	+	o	—	—	o	5	2	—	—
	11	—	—	—	+	o	—	—	+	o	—	+	—	o	+	—	8	3	—	—
	12	+	—	o	o	o	—	—	o	—	+	—	—	+	o	+	9	7	—	—
	13	—	+	o	o	o	o	o	o	o	o	+	o	—	+	o	1	11	—	—

* + = infection; — = no infection: o = no test.
† Lines grouped according to reaction with parents.

Here again, as in Table II, only the production of chlamydospores is considered in determining the number of sexual groups. If the degree of infection also were considered, lines 8 and 13 would be classed as different, as 13 formed less virulent combinations with Minn. D and with A12 x D.12 than did 8.

During the winter of 1928-29 inoculations were made in the greenhouse with lines from Minn. A13 x Minn. D. The results indicated that there were many sexual groups, and that some lines caused infection when inoculated singly into corn plants. Consequently, it was deemed advisable to make a more extensive test in the field. In the summer of 1929, therefore, the combinations indicated in Table IV were made. Thirty-one f_1 lines from Minn. A13 x Minn. D were paired with the parents; with certain other f_1 lines from the same cross; with Minn. F; with two f_1 lines from Minn. A13 x Minn. F; and with Minn. A6-1, which, like Minn. A13 is a mutant of Minn. A. Certain combinations also were made between the testers. In addition, each line was inoculated singly into corn plants. For each combination

25 to 40 plants, each, of normal Golden Bantam and Gehu corn, 8 to 12 inches tall, were inoculated. Ample checks, which remained uninfected, were injected with sterile nutrient solution. In addition, the inoculations with unpaired lines actually served as checks. The results are summarized in Table IV.

TABLE IV

RESULTS OF INOCULATING GOLDEN BANTAM AND GEHU CORN IN THE FIELD WITH f_1 LINES FROM MINN. A13 x MINN. D, WITH SIMILAR LINES FROM MINN. A13 x MINN. F, AND WITH CERTAIN OTHER LINES OF *Ustilago zeae*, IN COMBINATIONS WITH ONE ANOTHER

f_1 lines		Lines and infection*																Group‡
		Minn. A13 x Minn. D.									A13 x F.6	A13 x F.9	Minn. A6-1	Minn. A13	Minn. D	Minn. F	o†	
		1	4	14	17	19	22	25	30	31								
Minn. A13	32	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
x	31	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	2
Minn. D.	30	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	3
	4	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	4
	16	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	
	14	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	5
	19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	6
	26	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	
	1	—	—	—	—	—	+	—	—	—	—	+	—	—	—	—	—	7
	2	—	—	—	—	—	+	—	—	—	—	+	—	—	—	—	—	
	5	—	—	—	—	—	+	—	—	—	—	+	—	—	—	—	—	
	7	—	—	—	—	—	+	—	—	—	—	+	—	—	—	—	—	
	21	—	—	—	—	—	+	—	—	—	—	+	—	—	—	—	—	
	28	—	—	—	—	o	+	—	—	—	—	+	—	—	—	—	—	
	3	—	—	—	—	+	—	—	—	—	—	—	+	—	—	—	—	8
	17	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	—	9
	18	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	—	
	12	+	+	—	—	—	—	—	—	—	+	—	—	—	—	—	—	10
	13	—	+	—	—	—	—	+	—	—	+	—	—	—	—	—	—	11
	23	—	—	—	—	—	+	—	—	+	—	+	—	—	—	—	—	12
	24	—	—	—	—	—	+	—	—	—	—	+	+	—	—	—	—	13
	25	—	—	—	—	—	+	—	—	—	—	+	+	—	—	—	—	
	20	+	+	—	—	—	—	+	—	—	+	—	—	—	—	—	—	14
	22	+	+	—	—	—	—	+	—	—	+	—	—	—	—	—	—	
	11	—	—	—	—	+	+	+	+	—	—	—	—	+	—	+	—	15
	15	+	+	—	—	—	+	+	+	—	+	—	—	—	—	—	—	16
	27	+	+	—	—	—	+	+	—	—	+	—	—	—	—	+	—	17
	8	+	+	+	—	—	—	+	—	—	—	—	—	—	+	+	—	18
	6	+	+	+	+	+	+	+	+	+	o	+	o	+	+	+	+	19
	9	+	+	o	o	+	+	+	+	+	o	o	+	+	o	+	+	
	10	+	+	+	+	+	+	o	o	+	+	+	o	+	o	+	+	
A13 x F.6		—	—	—	—	—	+	—	—	—	—	+	o	—	—	—	—	7
A13 x F.9		+	—	—	—	—	—	+	—	—	+	—	—	—	—	—	—	20
Minn. A6-1		—	—	+	—	—	—	+	—	+	o	—	—	—	+	+	—	21
Minn. A13		—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	—	22
Minn. D		—	—	—	+	—	—	—	—	—	—	—	+	+	—	—	—	23
Minn. F		—	—	—	+	+	—	—	—	—	—	—	+	+	—	—	—	24

* + = infection; — = no infection; o = no test.

† Results of inoculations with unpaired lines.

‡ Based on reactions indicated in horizontal columns only.

It will be seen from Table IV that the 31 f_1 lines from A13 x D, listed vertically, fall into 19 groups on the basis of their reactions with the lines listed horizontally. Two lines, 17 and 18, appear to be identical with A13; line 18 may be, but 17 is not because A13 combines with 11, and 17 does not (compare vertical columns in the table). None of the lines are like Minn. D, the other parent. The groupings, indicated in Table IV, do not necessarily bring together identical lines, as shown by the apparent but not real identity of 17 and A13 when the horizontal columns only are considered. Again, lines 4 and 16 combined with only one of the lines listed horizontally and appear to be the same, but in reading the table vertically it is evident that line 4 combines with lines 8, 12, 13, 15, 20, 22, and 27. As line 16 was not paired with all of the lines listed vertically, there is no way of knowing whether it belongs to the same group as 4. Had all possible combinations been made, additional sexual groups probably would have become evident. In any case, the minimum number of sexual groups resulting from A13 x D is 19, including the group that cause infection singly. There appear, therefore, to be multiple factors for sex.

A13 x D.6, 9, and 10 caused infection when injected singly into corn plants. As the degree of infection was no weaker when these lines were used alone than when they were combined with other lines, it seems likely that they did not unite with them sexually. It is not known whether these lines satisfy the criteria for true homothallism, i.e., bisexuality. They may complete their life cycle in the haplophase; or possibly the nucleus in the sporidia of these lines is diploid; the fusion nucleus in the chlamydospores may not have undergone reduction division. If so, the lines are merely parthenogenetic. A study of their cytology is now under way.

There were decided differences in the degree of infection caused by the different combinations of lines. All combinations with line 11 were very weak pathogenically, incipient galls only being produced with lines 22 and 25, very light infection resulting with Minn. F and lines 19 and 30, and light infection with Minn. A13. Line 1 caused heavy infection in combination with six lines, and very light infection with one. Again, line 27 caused heavy infection in combination with three lines and very light infection with three others. The results indicate that there are multiple factors for pathogenicity as well as for sex.

Further Experiments with Lines That Caused Infection Singly

As it appeared from the previous experiments that Minn. A13 x Minn. D.6, 9, and 10 could cause infection singly, another field test was made in August, 1929. The results are given in Table V. A high percentage of infection resulted from inoculations with these monosporidial lines, as indicated by marked coloration on the leaves. More than 50 per cent of the plants inoculated with A13 x D.6 developed normal smut galls. The plants were rather small at the time of inoculation, and it was dry and hot for two weeks subsequently. This may possibly account for the relatively low percentage of plants with galls. There was no indication of any contamination. Not a single smut gall developed on plants inoculated with two unisexual lines, Minn. F and Minn. A13 x Minn. F.1. It appears certain from these experiments, therefore, that A13 x D.6, 9, and 10 cause infection singly, and Minn. A12 x Minn. D.6 appears to be decidedly more virulent than the other two.

TABLE V

Results of Inoculating Golden Bantam Corn in the Field with 'Homothallic' Lines and with Minn. F, and with Minn. A1 3x Minn. F.1

Lines	No. plants inoculated	No. plants infected	No. plants with galls
Minn. A13 x Minn. D.6	79	77	41
do 9	73	64	11
do 10	83	80	15
Check—Minn. A13 x Minn. F.1	66	0*	0
Check—Minn. F	40	0*	0
Check†	55	0	0

* When this line is paired with a line of opposite sex strong infection results.

† Plants inoculated with sterile nutrient solution.

In order to make absolutely certain that the results were not due to mixtures in the cultures, resulting from contamination with lines of another sex, or from sex mutation, several monosporidial isolations were made from each line in the usual manner. These subcultures were tested in the greenhouse, as indicated in Table VI. Many of the Golden Bantam plants inoculated with the sub-monosporidial cultures of Minn. A13 x Minn. D.6, 9, and 10 developed normal smut galls. However, some of the results were erratic. No infection resulted when Golden Bantam plants were inoculated with the following sub-monosporous cultures: A13 x D.9.1, A13 x D.10.4, and A13 x D.10.6. In a preliminary test, however, subculture Minn. A13 x Minn. D.6.2 was found to be virulent, having caused infection and produced large galls on two out of three plants 12 inches high. It is difficult to explain these results; they may have been due to mutation of the organism, which is known to be common in these three lines. It is possible also that the reduction division of the diploid nucleus did not occur in the usual manner in the promycelium, that the primary sporidia were diploid, and that reduction division occurred in some but not in others during the process of budding. Some sporidia would then be diploid and some haploid.

The evidence that lines 6, 9, and 10 cause infection singly seems conclusive. Betwen 500 and 600 plants of Golden Bantam and Gehu were inoculated with each line, and there was a high percentage of infection. The experiment was repeated, with similar results. Finally, monosporidial cultures again were made from the above monosporidial lines, and when inoculated into corn plants these lines also caused infection, with the exceptions noted. A cytologic study of these lines has not yet been made, but, whatever the nuclear condition, it is certain that some monosporidial lines can alone cause infection, with the production of galls containing chlamydospores. This ability seems to be rare in the Ustilaginales, altho Boss (1) states that *Ustilago ischaemi* completes its life cycle in the haplophase, both in artificial cultures and in nature.

TABLE VI

Results of Inoculating Golden Bantam Corn in the Greenhouse with Sub-Monosporidial Cultures Isolated from Cultures of Three 'Homothallic' Lines

Lines	No. plants inoculated	No. plants infected	No. plants with galls
Minn. A13 x Minn. D.6.1	26	19	11
do .2	22	1	1
do .3	19	16	13
do .4	25	16	9
do .5	19	12	9
Minn. A13 x Minn. D.9.1	16	0	0
do .2	19	2	1
do .3	19	2	2
do .4	20	5	1
do .5	19	8	4
do .6	14	6	2
Minn. A13 x Minn. D.10.1	16	14	8
do .2	22	3	2
do .3	20	10	4
do .4	24	0	0
do .5	15	5	0
do .6	10	0	0
Check-Minn. A13 x Minn. F.7	25	0	0
do .9	9	0	0
Check-Minn.A1	22	0	0

Cultural Characters

All the f_1 lines from the six crosses were studied comparatively on solid media. A general summary of their characteristics is given in Table VII, and a more detailed summary of the character of lines from Minn. A13 x Minn. F are given in Table VIII. Most of the lines of a given cross were strikingly different from their parents and from each other in one or more of the following characters: type and rapidity of growth, color, topography of colonies, production of sporidia and aerial mycelium, and tendency to mutate. Some of the differences between lines are illustrated in Plates II and III. It is interesting to note that the differences between the f_1 lines were as great as those between the lines obtained from many different countries.

TABLE VII

A COMPARISON OF THE CHARACTERISTICS OF THE f_1 LINES FROM SIX DIFFERENT CROSSES WITH THE CHARACTERISTICS OF THE PARENTAL LINES

Crosses	No. F_1 gametes isolated	No. sexual groups	Type of growth*				Cultural characters†			No. f_1 lines mutating	Color‡
			Crosses	f_1 lines							
				S	SM	M	Similar to parents	Similar to each other	No. different types of colonies		
Minn. A13 x Minn. F	13	At least 6	S x M	7	2	4	0	7 and 8 12 and 13	11	8	1 like Minn. F, 1 like Minn. A13, 9L, 2D
Minn. A13 x Minn. D	32	Many	S x M	11	7	14	0	23 and 24	31	21	4 like Minn. A13, 17L, 3D, 8I
Minn. A13 x Canada A	5	—§	S x M	3	2		0	0	5	5	1 like Minn. A13, 1 like Canada A, 1L, 2D
Minn. A x Canada A	25	—	M x M	21	2	1	—	—	—	15	7 like Minn. A, 8 like Canada A, 10D
Minn. A12 x Minn. D	13	At least 9	M x M	1		12	1 like Minn. A12	0	13	8	2 like Minn. A12, 7L, 4D, 1I
Minn. A x Minn. F	14	—	M x M	1		13	0	5 and 6 12 and 13	12	5	3L, 5D, 6I

* M = mycelial; S = sporidial; SM = semi-mycelial.

† Cultural characters include topography, surface, and margin.

‡ L = lighter than the lighter parent; D = darker than the darker parent; I = intermediate between light and dark parent.

§ — = no test.

None of 77 lines obtained from Minn. A13 x Minn. F, Minn. A13 x Minn. D, Minn. A13 x Canada A, Minn. A12 x Minn. D, and Minn. A x Minn. F were like their parents in cultural characteristics. (See Table VII.) It is unfortunate that cultural characteristics of f_1 lines from Minn. A x Canada A were not recorded. A number of these were quite similar to, if not identical with, each other, and some resembled closely the cultural characters of the parents. Among the f_1 lines from Minn. A13 x Minn. F and from Minn. A x Minn. F there were two sets of duplicates each; from Minn. A13 x Minn. D, one; and none of those from Minn A13 x Canada A and Minn. A13 x Minn. D were alike. Mutants Minn. A12 and Minn. A13 when crossed with the same line, Minn. D, gave rise to f_1 lines which were all different from each other. The results indicate that multiple factors govern most cultural characters.

From the cross Minn. A12 (mycelial) x Minn. D (mycelial) 12 sporidia (F_1 gametes) produced mycelial colonies, and only one a sporidial colony. Minn. A13 (sporidial), a sister mutant to Minn. A12 (mycelial), crossed also with Minn. D (mycelial) gave rise to 14 mycelial, 7 semi-mycelial, and 11 sporidial types. In another cross, Minn. A13 (sporidial) x Minn. F (mycelial), the sporidial types predominated over those of the mycelial type. But Minn. F (mycelial) x Minn. A (mycelial), the parent of Minn. A13, gave rise to 1 sporidial and 13 mycelial f_1 lines. It seems evident from these breeding tests that the mutants Minn. A12 (mycelial) and Minn. A13 (sporidial) are genetically different from each other, and A13 is different from its parent, Minn. A. It is significant that Minn. A crossed with Minn. F and with Minn. D gave rise to different ratios of mycelial to sporidial types. Therefore, Minn. F and Minn. D apparently do not carry the same genetic factors for type of growth.

There apparently are multiple factors for color of colonies. Of the 32 f_1 lines from Minn. A13 x Minn. D, 17 were lighter than either parent; 3 were distinctly darker than the darker parent; 4 were like one parent, Minn. A13, in color; and the other 8 were intermediate in color between the light parent and the dark parent. Twenty-six of the 32 lines produced colonies distinctly different in color from each other. Minn. A12 x Minn. D.7 was conspicuously darker than the darker parent, which was reddish brown. A12 x D.7 was coal black and gave rise almost immediately to several pure white mutants, that have remained white for several generations. There also was one blackish line among the 25 isolated from Canada A x Minn. A. Both parents in this case were cream to tan in color. Seven gametic lines from the same cross resembled one of the parents in color, and 8 the other parent. None were lighter than the parents, but 10 were darker than either parent. Among the lines obtained from all the crosses, with the exception of Canada A x Minn. A, there were many kinds and gradations of color. The evidence tends to show that multiple factors are concerned in color production. The results indicate also that the mutants, Minn. A12 and Minn. A13, do not possess the same factors for color as their parent Minn. A.

Mutability

Some of the lines derived from six crosses listed in Table VII mutated frequently; others did not mutate during the first cultural generation in flasks. (See Table VIII.) It is obvious that Minn. A13 x Minn. F.1 and Minn. A13 x Minn. F.11 were very unstable. Three colonies of the former gave rise to 16 mutants, 4 of which were different; and the latter line produced more than 20 mutants, 5 of which were distinctly different from the parent and each other. The f_1 lines from Minn. A13 x Canada A were the least stable; they gave rise to the largest number of mutants per colony, while those from Minn. A x Minn. F apparently were the least mutable of the six crosses studied.

TABLE VIII

CULTURAL CHARACTERISTICS OF THIRTEEN f_1 LINES FROM MINN. A13 x MINN. F AND OF THE PARENTAL LINES WHEN GROWN ON NUTRIENT MEDIA

Parents and f_1 lines*	Diam. in mm.	Growth on potato-dextrose agar			Sporidia production in 1 per cent malt + 1 per cent sucrose solution
		Type†	Color‡	No. sectors	
Minn.F	46	M	Lilac	0	Light
Minn. A13	36	S—	Cream-tan	7	Abundant
Minn. A13 x Minn. F.1	36	S+	D	16	do
do 2	46	M	Cream-tan	1	do
do 3	37	S+	D	2	do
do 4	50	M	L	0	do
do 5	43	S	Lilac	0	do
do 6	34	S+	L	0	do
do 7	41	Sm	L	0	do
do 8	41	Sm	L	0	do
do 9	33	S+	L	4	do
do 10	36	S	L	9	do
do 11	40	S	L	20+	do
do 12	47	M	L	1	Moderate
do 13	50	M	L	0	do

* All segregates of different colors, except that 7 was similar to 8.

† S = sporidial; M = mycelial; Sm = semi-mycelial.

‡ D = darker than the lilac parent; L = lighter than the cream-tan parent.

+ and — indicate degrees of the type indicated.

Pathogenicity

The author is of the opinion that, while the proper complement of sex factors in the dikaryons is normally essential to enable *U. zeae* to parasitize the corn plant successfully, there are factors for pathogenicity in addition to those for sex. This fact became clearly evident in observing the degree of infection caused by the various combinations listed in Tables II, III, and IV. The various dikaryophytes that formed chlamydospores were by no means equally virulent. Some caused heavy infection, some light, and others very light infection.

The degree of infection is not recorded in Tables III and IV because the facts are shown clearly in subsequent tables.

The three lines that cause infection singly also appear to differ in virulence, altho all of them can produce chlamydospores. A13 x D.10 caused light or very light to incipient infection throughout, while line 6 caused heavy infection in most cases. In the discussion of Table IV evidence of differences in pathogenicity of different combinations of lines also is given. Additional experiments were made and the results recorded in Tables IX and X.

TABLE IX

Results of Inoculating Six Selfed Lines of Corn in the Greenhouse with f_1 Lines from Minn. A13 x Minn. F and with the Parental Lines in Combination with One Another

Selfed lines of corn	Minn. A13 x Minn. F	(Minn. A13 x Minn. F.1) x (Minn. A13 x Minn. F.9)	(Minn. A13 x Minn. F.6) x (Minn. A13 x Minn. F.9)
	Infection*	Infection	Infection
S-1	$\frac{8}{50}$ L	$\frac{35}{35}$ H	$\frac{41}{42}$ H
S-2	$\frac{5}{44}$ L	$\frac{30}{30}$ H	$\frac{23}{24}$ H
S-3	$\frac{3}{43}$ I	$\frac{21}{21}$ L	$\frac{21}{26}$ M
S-4	$\frac{7}{41}$ L	$\frac{22}{22}$ H	$\frac{28}{28}$ H
F-1	$\frac{3}{20}$ I	$\frac{18}{18}$ L	$\frac{32}{36}$ L
F-2	$\frac{2}{28}$ I	$\frac{18}{30}$ I	$\frac{32}{32}$ L

*The denominator denotes the number of plants inoculated; the numerator, the number infected.

H = heavy infection; M = moderate; L = light; I = incipient, i.e., galls very small and wart-like.

During the winter of 1928-29 a comparative pathogenicity test was made in the greenhouse with the following combinations: (Minn. A13 x Minn. F.1) x (Minn. A13 x Minn. F.9); (Minn. A13 x Minn. F.6) x (Minn. A13 x Minn. F.9), and the parental lines, Minn. A13 x Minn. F. Six selfed lines of corn were inoculated when about 8 to 12 inches high. The results are given in Table IX. Combinations of the two f_1 lines proved to be much more virulent than the parental combination. This may not be a fair comparison as far as the relative pathogenicity of the parental combination and that of the f_1 lines is concerned, because at the time the original cross, Minn. A13 x Minn. F, was made in the winter of 1928, the parental lines were strongly pathogenic, while subsequent tests proved that Minn. A13 had lost some of its original virulence. The results do show, however, that the pathogenicity of different combinations may be quite different.

A more extensive test on parasitism was made in the field. The combinations mentioned above were used. In addition, Minn. A13 x Minn. F.7 was back crossed with Minn. F; and Minn. A, the parent of Minn. A13, also, was crossed with Minn. F. Ten selfed lines of sweet corn were inoculated with the five combinations. The corn plants were 18 to 24 inches high and jointing at the time of inoculation. Duplicate plots were inoculated with each combination. The data are presented in Table X. There were decided differences in the virulence of the different combinations. In descending order of virulence, they rank as follows: (Minn. A13 x Minn. F.6) x (Minn. A13 x Minn. F.9); (Minn. A13 x Minn. F.1) x (Minn. A13 x Minn. F.9); (Minn. A13 x Minn. F.7) x Minn. F. The other two combinations were relatively weak in virulence. The results were consistent in both series.

TABLE X

RESULTS OF INOCULATING TEN SELFED LINES OF CORN IN THE FIELD WITH f_1 LINES FROM MINN. A13 x MINN. F, IN COMBINATION WITH ONE ANOTHER OR WITH MINN. F, AND WITH THREE OTHER MONOSPORIDIAL LINES IN COMBINATION WITH ONE ANOTHER

Selfed lines of corn	(Minn. A13xMinn. F.1)x (Minn. A13xMinn. F.9)	(Minn. A13xMinn. F.6)x (Minn. A13xMinn. F.9)	Minn. F x (Minn. A13xMinn. F.7)
	Infection*	Infection	Infection
S-4	$\frac{21}{32}$ L to M ±	$\frac{33}{40}$ L to H +	$\frac{27}{37}$ L to M +
S-5	$\frac{30}{32}$ I to M ±	$\frac{28}{29}$ L to H ++	$\frac{14}{24}$ I to M +
S-6	$\frac{24}{27}$ L to H ±	$\frac{28}{30}$ L to H ++	$\frac{17}{30}$ I to L ±
S-7	$\frac{11}{17}$ I to L ±	$\frac{21}{21}$ H +++	$\frac{11}{16}$ I to L ±
S-8	$\frac{19}{32}$ L to M ±	$\frac{29}{29}$ M to H ++	$\frac{19}{30}$ I to L ±
S-9	$\frac{7}{24}$ L to M ±	$\frac{22}{23}$ L to H +++	$\frac{11}{21}$ L to M +
S-10	$\frac{5}{31}$ I to L ±	$\frac{25}{32}$ I to H +	$\frac{12}{30}$ I to L ±
S-11	$\frac{16}{28}$ I to L ±	$\frac{31}{33}$ M to H ++	$\frac{17}{29}$ I to L ±
S-14	$\frac{10}{19}$ L to M ±	$\frac{23}{23}$ L to H ++	$\frac{5}{16}$ I ±
S-15	$\frac{32}{33}$ L to H ±	$\frac{36}{36}$ L +++	$\frac{18}{23}$ ± to M +

TABLE X—*Continued*

Selfed-lines of corn	Minn. A13 x Minn. F	Minn. A x Minn. F	Checks†
	Infection	Infection	Infection
S-4	$\frac{3}{25}$ I to L ±	$\frac{3}{25}$ L ±	$\frac{1}{22}$ L +
S-5	$\frac{6}{17}$ I ±	$\frac{6}{25}$ I to L ±	$\frac{0}{16}$
S-6	$\frac{5}{26}$ I to L ±	$\frac{5}{17}$ I to L ±	$\frac{0}{17}$
S-7	$\frac{2}{14}$ I to L ±	$\frac{5}{20}$ I to L ±	$\frac{0}{12}$
S-8	$\frac{8}{34}$ I to L ±	$\frac{8}{26}$ I to L ±	$\frac{1}{18}$ L ±
S-9	$\frac{9}{22}$ L ±	$\frac{5}{21}$ L to M ±	$\frac{0}{16}$
S-10	$\frac{3}{29}$ L ±	$\frac{2}{25}$ I to L ±	$\frac{0}{19}$
S-11	$\frac{4}{26}$ I to L ±	$\frac{4}{29}$ I to L ±	$\frac{0}{20}$
S-14	$\frac{5}{21}$ I to L ±	$\frac{2}{20}$ I ±	$\frac{0}{21}$
S-15	$\frac{11}{29}$ I to L ±	$\frac{12}{28}$ I to L ±	$\frac{0}{21}$

* The denominator denotes the number of plants inoculated; the numerator, the number infected. Plus and minus signs indicate the number of galls; +++ indicate very many galls; — indicates few galls.

H=heavy infection; M=moderate; L=light; I=incipient, i.e., galls very small and wart-like.

† Inoculated with Minn. A13 x Minn. F.6.

It appears certain from all of the observations and experiments that there are multiple factors for pathogenicity and that the virulence of the pathogene in the field depends on the chance combinations of gametic lines with the proper complement of factors for pathogenicity and sex.

CONCLUSIONS

The results of experiments with combinations of monosporidial lines substantiate the previous conclusions of Christensen and Stakman (2) that there are parasitic races or physiologic forms of *U. zeae*, and that selfed lines of corn may be physiologically resistant to some forms and susceptible to others. The degree of infection depends upon the lines of smut and the lines of corn involved. It is clear that the pathogenicity of combinations of lines probably is the component of the factors for pathogenicity, and to a certain extent of those for sex, of the smut lines causing infection. A monosporidial line of *U. zeae* may be strongly pathogenic in combination with certain lines of opposite sex and only weakly pathogenic with other lines of opposite sex. It seems clear that different lines have different factors for pathogenicity, apart from those for sex. The most conclusive evidence, however, that monosporidial lines differ with respect to pathogenicity as such, is the fact that those which can cause infection alone also have different degrees of virulence.

While it was shown that some monosporidial lines, alone, can cause infection, it seems evident that *U. zeae* is predominantly heterothallic. As there evidently are multiple factors for sex and pathogenicity, there may be a great many different combinations of sexual and pathogenic potentialities. While the ultimate implication of these facts depends upon the number of factors in existence, it is significant that so many different combinations are possible. *U. zeae* is very heterozygous for most characters. This means that great variation is possible and that there may be a large number of combinations resulting in the production of a great many different lines.

There is still further evidence from the results recorded here that haploid lines are clones and that the so-called mutations are due to genotypic changes. The corn smut pathogene, therefore, comprises many lines now, and new ones continually are arising by mutation and hybridization. It seems likely that attempts should be made to produce lines of corn with functional or structural resistance. It is possible that some lines of corn may have physiologic resistance to all of the combinations of physiologic forms with which they are likely to be inoculated under natural conditions. However, it seems probable that lines of corn with functional or structural resistance will be most useful. There is some evidence that such lines are in existence, but information regarding the mode of infection and the nature of resistance still is very meager. Therefore, much more investigation is necessary before the practical implications of the results obtained can be known.

SUMMARY

1. Monosporidial lines from Canada, France, Hungary, Italy, Spain, and from several places in the United States produced smut galls when paired with two monosporidial lines of opposite sex isolated from chlamydospores from Minnesota. There was no evidence, however, of complete interfertility or intersterility between possible "Geographic strains."

2. Chlamydospores were obtained from six different crosses of

monosporidial lines, including some mutants. One hundred and two sporidia (F_1 gametes) from these crosses were isolated and the resulting monosporidial lines (designated as f_1 lines) were studied in considerable detail.

3. A study of these f_1 lines on potato-dextrose agar indicates that there are multiple factors in *U. zeae* for rate of growth; for type of growth; for color, consistency, and topography of colonies; and, possibly, for the tendency to mutate. Thirty-two f_1 lines isolated from chlamydospores in a single smut gall resulting from crossing two monosporidial lines were all culturally different from each other.

4. There apparently are multiple factors for sex and pathogenicity.

5. Dikaryophytes resulting from pairing f_1 lines from a single cross may have various degrees of pathogenicity: some are very virulent, some moderately virulent, and others appear to be relatively innocuous.

6. *U. zeae* is predominantly heterothallic but three monosporidial lines obtained by isolating F_1 gametes from a cross cause normal infection when inoculated singly into corn plants, although they have different degrees of virulence. Thirty-one other lines from the same cross did not cause infection when inoculated singly into corn.

7. A study of the growth type of f_1 lines isolated from crosses between certain mutants and their parents and between the mutants and another monosporidial line indicates rather clearly that the so-called mutants are true mutants resulting from genotypic changes.

8. It will be necessary to learn more about the mode of infection, the nature of resistance of lines of corn to smut, and the performance of these lines in the field before the practical importance of the facts presented in this paper can be known.

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PLATES

PLATE I

Golden Bantam Corn Inoculated with Monosporidial Lines of *Ustilago zeae*.

On the left, Minn. A13 x Minn. D.6.1. On the right, Minn. A13 x Minn. D.6.2.3. Both lines caused normal infection when inoculated singly into the corn plants. So far only three lines have been found that can cause infection singly.

PLATE I

PLATE II

Eight monosporidial f_1 lines from cross, Minn. A13 x Minn. D, on potato-dextrose agar, showing differences in cultural characteristics.

PLATE II

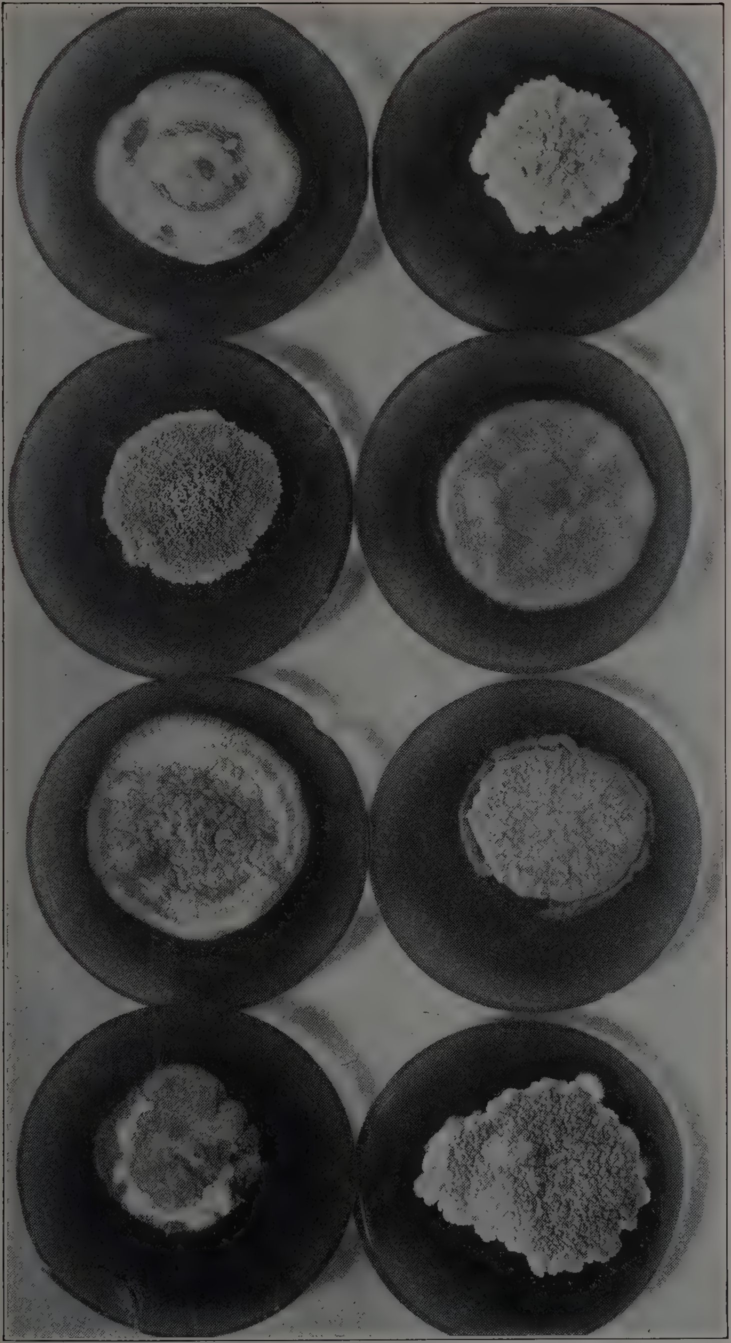
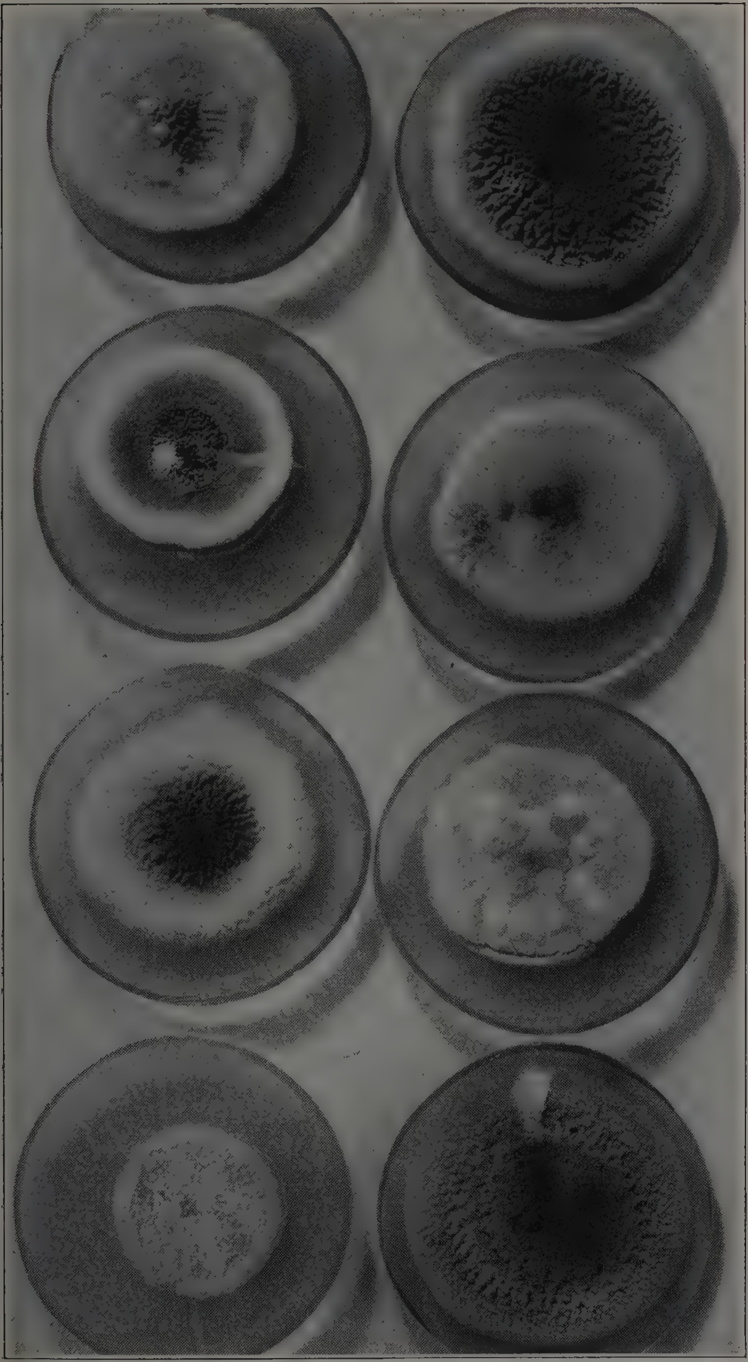


PLATE III

Eight monosporidial f_1 lines from cross, Minn. A12 x Minn. D, on potato-dextrose agar, showing differences in cultural characteristics.

PLATE III



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University of Minnesota
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Identification of Cultivated Raspberries

J. D. Winter
Division of Horticulture

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IDENTIFICATION OF CULTIVATED RASPBERRIES

J. D. Winter

INTRODUCTION

According to Bailey (1898) the raspberry has been cultivated in Europe since the fourth century. Varieties of European origin are mentioned in American literature as early as 1806. Bailey states that the native American raspberry was first brought into cultivation about 1825. This was a purple variety. Cultivation of the black raspberry began about 1832 and the American red raspberry was first cultivated about 1860.

Nearly all raspberries cultivated for their fruit in North America are derived from the American and European red raspberries and from the American black raspberry *Rubus occidentalis* Linn. There is much difference of opinion among botanists whether or not the American red raspberry *Rubus strigosus* Michx. should be considered a subspecies of the European red raspberry *Rubus idaeus* Linn. In this bulletin they are treated as distinct species in accordance with Rosendahl and Butters (1927) and others. Hedrick (1925) considers *R. strigosus* a subspecies. All black varieties are derived from *R. occidentalis* and the purple raspberries are hybrids of red and black varieties. Several oriental species are grown to a limited extent. The Japanese wineberry *Rubus phoenicolasius* Maxim. and the strawberry-raspberry *Rubus illecebrosus* Focke, are the best known of the oriental species.

CHARACTERS USED TO IDENTIFY RASPBERRY SPECIES

Red raspberries are usually distinguished from black raspberries by the color of the fruit and by the erect canes that are more or less covered with straight, stiff, bristle-like prickles. When referring to red raspberries these are called bristles in this bulletin to distinguish them from the typical prickle of the black raspberry, altho botanically both are prickles. The canes of the black raspberry are erect and arching with few to many prickles that are usually more or less hooked. A few cultivated varieties are almost without prickles. Varieties which produce amber-white fruit occur in both the red and the black raspberry.

The European raspberry *R. idaeus* is distinguished from *R. strigosus* by heavier and more rugose foliage and by the absence of stalked glands. The canes of *R. strigosus* are more slender and usually darker in color. The following comparison is taken from descriptions by Hedrick (1925) and by Rosendahl and Butters (1927).

The young canes of *R. idaeus* are often finely tomentose, becoming glabrate and are not bristly to the top. The inflorescence is more or less bristly but without glands; the peduncles and pedicels are finely pubescent. Stalked glands are not found on the canes. The hypanthium is broad and easily seen in the open flower; the stamens are erect. The sepals are tomentose and often bear a few hooked prickles. The style is not so slender as the style of *R. strigosus*. The fruit is dark red or yellow, thimble-shaped, and is produced more or less continuously throughout the season.

The young canes of *R. strigosus* are typically without pubescence and are bristly to the top. The inflorescence is glandular, and more or less bristly; the peduncles and pedicels are not pubescent. Stalked glands are common on the canes. The hypanthium is narrow and concealed by the stamens which are incurved. The sepals are glandular and bristly; the style is very slender. The leaves are less tomentose beneath than the leaves of *R. idaeus*. The fruit is bright red or rarely yellow, and hemispherical.

Rosendahl and Butters (1927) call attention to a subspecies *R. strigosus* var. *canadensis* which occurs in northern Minnesota and is found from Labrador to Alaska. The pubescence of this subspecies is typical of *R. idaeus* and occasional specimens occur with few or no glandular bristles. The floral characters, however, resemble *R. strigosus* rather than *R. idaeus*. It is noteworthy that Grubb (1922) reports that both glabrous and pubescent forms of the wild red raspberry occur in England.

DERIVATION OF OUR CULTIVATED RASPBERRIES

Examination of the following cultivated varieties indicate that the majority have been derived from hybrids of *R. idaeus* and *R. strigosus*. Darrow (1920) working with a somewhat different list of varieties concluded that most of the cultivated red raspberries grown in North America at the present time are derived either directly from *R. strigosus* or are hybrids between that species and *R. idaeus*. The fact that a variety is typically of the *R. strigosus* type does not preclude the possibility of its being derived partly from *R. idaeus*. Of the intermediate group the Cuthbert, Golden Queen, and Herbert show most evidence of the *R. idaeus* type.

R. strigosus	*R. strigosus* x *R. idaeus*		*R. idaeus*
Chief	Cuthbert	Latham	La France
King	Eaton	Loudon	Lloyd George
Ohta	Golden Queen	Marlboro	
Ranere (St. Regis)	Herbert	Newman	
Sunbeam	June	Viking	

IDENTIFICATION OF HORTICULTURAL VARIETIES

Those who are familiar with raspberry-growing do not find it difficult to recognize varieties in the field during the growing season. It is much more difficult to assemble and classify the characters on which the recognition is based. Some characters are extremely variable and are influenced by location, soil, climate, and plant diseases.

In a previous paper on the identification of raspberry varieties, the writer (1925) describes certain characters which were found to be relatively constant under varying conditions of growth. Attention was called to the abundance, color, and structure of the bristles; the number and form of the leaflets; the color of the foliage; the presence or absence of glaucous bloom.

Owing to the frequent occurrence of hybrids between *R. strigosus* and *R. idaeus* many of the botanical characters which separate these species can be used to identify horticultural varieties. It is important to observe that the young canes differ in some characters from the fruiting canes of the same variety, as for example in the number of leaflets. For this reason the young canes have been used for identification except when portions of the flowering stalk are referred to. The fruit has not been used as a primary factor in descriptions so that varieties may be identified at any time during the growing season. The differences between black raspberry varieties are less marked, probably because all the black varieties are derived from one species.

The shape of the foliage is relatively constant and may be used to separate varieties of the red raspberry. The leaflets of some

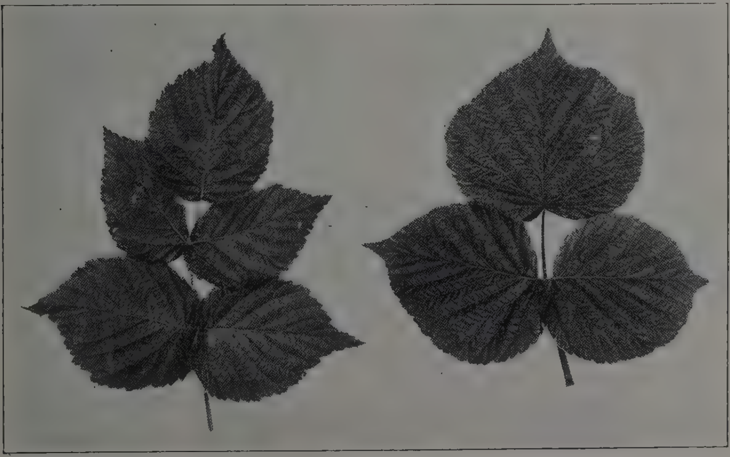

Fig. 1. Two Varieties of Red Raspberry Leaves
Right, Sunbeam, with broad terminal leaflets; left, Latham, with narrower leaflets.

varieties are broad, with the width of the terminal leaflet often equal to the length, or nearly so. The leaflets of other varieties are narrower, the width of the terminal leaflet being decidedly less than the length. Typical leaves are illustrated in Figure 1.

Stalked glands as illustrated in Figure 2 are characteristic of *R. strigosus* but not of *R. idacus.* They can be seen readily with a hand lens. In some varieties they are present on the cane, petiole, peduncle, pedicel, calyx, and other parts; in others only on some of these parts. Bristles on the young canes of most cultivated varieties generally are not glandular; however, those on the native *R. strigosus* usually are.

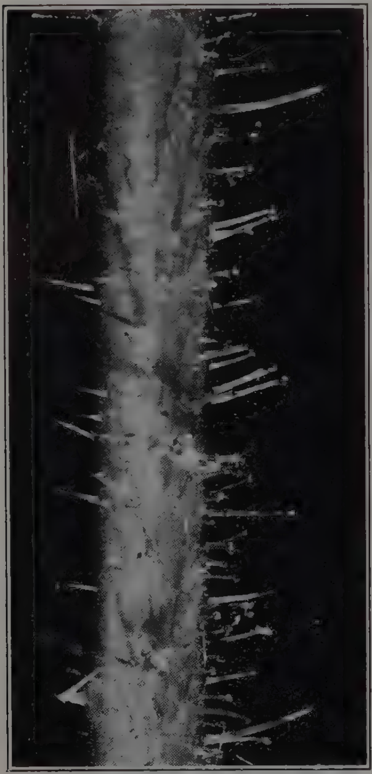

Fig. 2. Stalked Glands, Much Enlarged, on Petiole of Sunbeam Raspberry

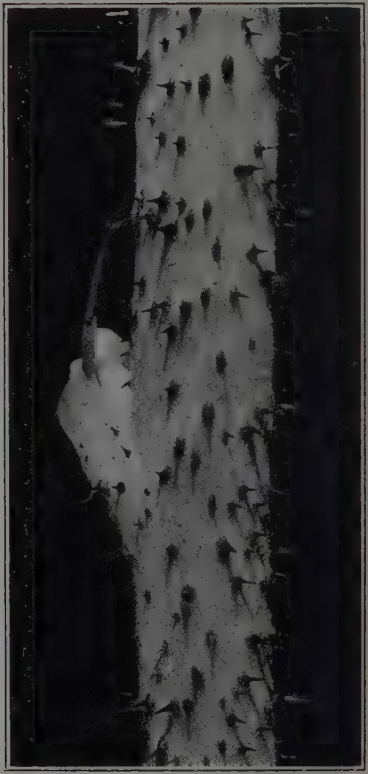

Fig 3. Young Cane Showing the Dark Base of the Bristles, Variety Lloyd George

In a few instances the only glands present are sessile or practically so, for example those on the petiole of Latham. They are found mostly at the junction of the lower pair of leaflets but are so small that they may easily pass unnoticed. They are much less conspicuous than the typical stalked glands of *R. strigosus.*

Stalked glands are not found on black or purple varieties, but extremely small sessile glands are common on the cane, petiole, pedicel, and calyx. It is noteworthy that typical stalked glands are common on the cane, petiole, pedicel; and calyx of the blackberry.

The general character and abundance of bristles on the cane, petiole, peduncle, pedicel, and calyx can be used in identification. Bristles on the lower portion of the cane are of little or no value for this purpose. Most varieties have many bristles within 6 to 12 inches of the ground and these are usually more slender and lack the individual character of those on the upper portion of the cane. This also is true of the bristles on very young canes.

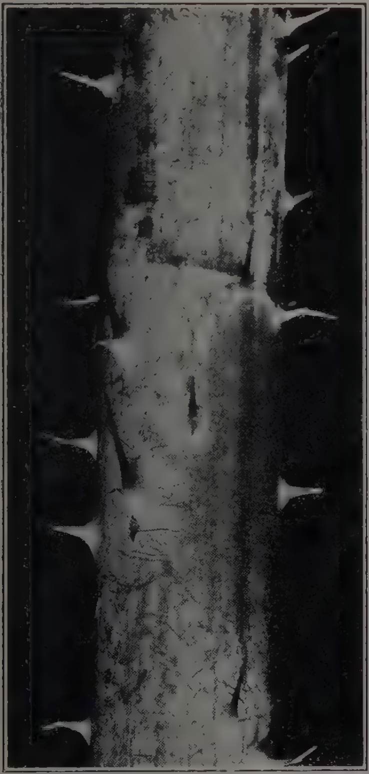

Fig. 4. Golden Queen, Showing Enlargement at the Base of the Bristles on the Young Cane

An abundance of bristles is typical of *R. strigosus* altho many cultivated varieties have few. Varieties may be divided into two groups, (1) those with many bristles on the petiole and (2) those without or with few (usually not exceeding 20 to 25).

The color of the bristle at its base is also characteristic and can be used in identification. Here again varieties may be divided into two groups, (1) those with bristles conspicuously darker at the base than the young cane as illustrated in Figure 3 and (2) those with bristles similar in color at the base.

The structure of the bristle or prickle is useful in identification. In some varieties the base of the bristle is markedly enlarged as illustrated in Figure 4 in contrast to the lack of any obvious enlargement in other varieties. The average length of the bristles or prickles is also helpful in identification.

Bristles are generally present on the calyx of red varieties and vary in number from few to many. The lack of bristles or prickles on the calyx of all black varieties examined indicates a characteristic difference in this respect between red and black varieties. The only purple raspberry observed, the Columbian, was found to have very few prickles on the calyx.

The color of the new growth at the tip of the cane is not a reliable character except to distinguish yellow fruited varieties. These do not show any indication of red at the tip. The amount of color shown at the tip of red varieties changes considerably according to location and season.

The number of leaflets comprising a single leaf is not sufficiently constant to use in identification and varies on the old and new canes of the same variety. Leaves of the young canes have either three or five leaflets; those of the flowering shoot invariably have only three.

Grubb (1922) mentions the appearance of pubescence at the tip of the new canes as the most constant character under all conditions of growth in England. This is not true of varieties most commonly grown in North America.

KEY TO 16 VARIETIES OF RASPBERRIES

The following key is based, in so far as possible, on cane and foliage characters. For purposes of identification young canes not less than half grown are used, as very young canes do not exhibit distinct varietal characters.

A. Canes erect, with few to many straight, stiff bristles; fruit red or yellow.

  B. Terminal leaflets on the young cane broad, width often equal to length or nearly so.

    C. Petiole of leaves near the tip of the young cane with bristles absent or few, usually not exceeding 20 to 25 bristles.

      D. Petiole of leaves on the young cane with many sessile glands, mostly at the junction of the lower leaflets and the petiole.

Canes medium height; moderately glaucous; bristles on the young cane very few; base of bristles about the same color as the young cane; bristles on the petioles near the tip of the young cane few, not gland-tipped, 0.5-1.0 mm. in length; petiole and pedicel glabrous; pedicel and calyx with many bristles, mostly gland-tipped; calyx finely tomentose; fruit red, conic, medium to large, firm, midseason; drupelets medium to large................**LOUDON**

      DD. Petiole of leaves on the young cane with sessile or stalked glands absent or very occasional.

Canes tall, very glaucous; leaves dark green, distinctly rugose; bristles on the young cane usually absent; bristles on the petioles near the tip of the young cane absent or very occasional, not gland-tipped, 0.5-1.0 mm. in length; petiole and pedicel glabrous; pedicel and calyx with very few bristles, not gland-tipped; calyx finely tomentose; fruit red, round, very large, firm, early; drupelets large. . . . . **JUNE**

CC. Petiole of leaves near the tip of the young cane with many bristles.

D. Bristles on the young cane with base usually much enlarged.

Canes tall, moderately to very glaucous; leaves dark green, distinctly rugose; bristles on the young cane extremely numerous; base of bristles about the same color as the young cane, distinctly enlarged; bristles on the petioles near the tip of the young cane numerous, mostly gland-tipped, 1.0-3.0 mm. in length; petiole and pedicel glabrous; pedicel and calyx with many bristles, mostly gland-tipped; calyx finely tomentose; fruit dark red, round, medium size, soft, decidedly acid, midseason; drupelets medium size. . . . . **SUNBEAM**

DD. Base of bristles on the young cane not conspicuously enlarged.

Canes medium tall, slightly glaucous, leaves medium green, not conspicuously rugose; bristles on the young cane numerous; base of bristles about the same color as the young cane; bristles on the petioles near the tip of the young canes common, mostly gland-tipped, 1.0-2.0 mm. in length; petiole and pedicel glabrous; pedicel and calyx with many bristles mostly gland-tipped; calyx finely tomentose; fruit red, round-conic, large, unusually firm, early; drupelets medium to small. . . . . **CHIEF**
(syn. *Minn. No. 223*)

BB. Width of terminal leaflets on the young cane decidedly less than the length.

C. Petiole of leaves near the tip of the young cane with bristles absent or few, usually not exceeding 20 to 25 bristles.

D. Bristles on the young cane absent or occasional.

Canes medium height, not obviously glaucous; bristles on the petioles near the tip of the young cane absent or occasional, not gland-tipped, 0.5-1.0 mm. in length; petiole of leaves on the young cane with many sessile glands, mostly at the junction of the lower leaflets and the petiole; petiole and pedicel glabrous; pedicel and calyx with many bristles, mostly gland-tipped; calyx finely tomentose; fruit dark red,

round-conic, very large, firm, rather acid, midseason, does not separate easily from receptacle; drupelets large................**EATON**
(syn. *Alton Improved, Crimson Beauty, Idaho, Iowa, Paragon*)

DD. Bristles on the young cane common to numerous.

E. Petiole of leaves on the young cane with many sessile glands, mostly at the junction of the lower leaflets and the petiole.

Canes tall, moderately to very glaucous; bristles on the young cane common; base of bristles about the same color as young cane; bristles on the petiole near the tip of the young cane few, not gland-tipped, 1.0-1.5 mm. in length; petiole and pedicel glabrous; pedicel and calyx with many bristles, mostly gland-tipped; calyx finely tomentose; fruit red, round, very large, firm, late midseason; drupelets medium size...............**LATHAM**
(syn. *Imogene, Minnesota No. 4, Redpath*)

EE. Petiole of leaves on the young cane with sessile or stalked glands absent or very occasional.

Canes tall, moderately glaucous; bristles on the young cane common; base of bristles about the same color as young cane; bristles on the petioles near the tip of the young cane very few, not gland-tipped, 0.5-1.0 mm. in length; petiole glabrous, pedicel finely pubescent; pedicel and calyx with many bristles, not gland-tipped, but with occasional sessile glands; calyx finely tomentose; fruit red, round-conic, large, firm, midseason; drupelets medium size....................**VIKING**

CC. Petiole of leaves near the tip of the young cane with many bristles.

D. Base of bristles conspicuously darker in color than the young cane.

Canes medium tall, moderately glaucous; terminal leaflets often 3-lobed; bristles on the young cane numerous; base of bristles red; bristles on the petioles near the tip of the young cane numerous, mostly gland-tipped, 1.0-3.0 mm. in length; petiole and pedicel glabrous; pedicel and calyx with many bristles, mostly gland-tipped; calyx finely tomentose; fruit red, round, medium size, rather soft, very early; drupelets medium size..**RANERE**
(syn. *St. Regis*)

DD. Base of bristles about the same color as the young cane.

E. Bristles on the petioles of the young cane mostly gland-tipped.

F. Bristles on the young cane common but not extremely abundant.

Canes tall, moderately glaucous, bristles on the young cane common; bristles on the petiole near the tip of the young cane common, frequently gland-tipped 1.0-1.5 mm. in length; petiole and pedicel glabrous; pedicel and calyx with many bristles, mostly gland-tipped; calyx finely tomentose; fruit red, round, large, firm, early; drupelets medium size.........**KING**

FF. Bristles on the young cane very numerous.

Canes tall, moderately to very glaucous; bristles on the young cane very numerous; bristles on the petioles near the tip of the young cane very numerous, mostly gland-tipped, 1.0-2.0 mm. in length; petiole and pedicel glabrous; pedicel and calyx with many bristles, mostly gland-tipped; calyx finely tomentose; fruit red, round, medium size, soft, rather acid, midseason; drupelets medium to small......**OTHA** (syn. *Flaming Giant*)

EE. Bristles on the petioles of the young cane not gland-tipped or rarely so.

F. Tip of new growth yellowish green.

Canes tall, moderately glaucous; terminal leaflets narrow; bristles on the young cane common, distinctly rigid and prickle-like; base of bristles about the same color as young cane; bristles on the petiole near the tip of the young cane, common, usually from 20 to 30 in number, not gland-tipped, or rarely so, 1.5-2.0 mm. in length; petiole glabrous; pedicel slightly pubescent; pedicel and calyx with few bristles, not gland-tipped; petiole of leaves on the young cane with occasional sessile glands, mostly at the junction of the lower leaflets and the petiole; similar sessile glands common on the pedicel and occasional on the calyx; calyx finely tomentose; fruit yellow, conic, medium to large, rather soft, midseason; drupelets small.................**GOLDEN QUEEN**

FF. Tip of new growth tinted with red.

G. Petiole of leaves on the young cane with many sessile glands, mostly at the junction of the lower leaflets and the petiole.

Canes tall, moderately glaucous; terminal leaflets narrow; bristles on the young cane common, distinctly rigid and prickle-like; base of bristle about the same color as young cane; bristles on the petiole near the tip of the young cane common, usually from 20 to 30 in number, not gland-tipped, 1.5-2.0 mm. in length; petiole glabrous; pedicel finely pubescent; pedicel and calyx with few bristles, not gland-tipped; sessile glands common on pedicel and occasional on calyx; calyx finely tomentose; fruit dark red, conic, large, firm, midseason; drupelets small .... **CUTHBERT**

GG. Petiole of leaves on the young cane with sessile or stalked glands absent or very occasional.

Canes tall, moderately glaucous; terminal leaflets moderately broad; bristles on the young cane numerous, quite rigid and prickle-like; base of bristles about the same color as the young cane; bristles on the petioles near the tip of the young cane common, usually from 20 to 30 in number, not gland-tipped, 1.0-1.5 mm. in length; petiole glabrous, exceptionally short; pedicel finely pubescent; pedicel and calyx with many bristles, not gland-tipped; calyx finely tomentose; fruit red, round-conic, large, rather soft, midseason; drupelets medium size .... **HERBERT**

AA. Canes recurving or spreading, with few to many prickles which are usually more or less hooked; fruit black or dull purple-red.

B. Prickles present on calyx.

Canes very tall, upright-spreading, moderately glaucous, with many very small sessile glands; leaves at tip of cane slightly tinted with red; straight or slightly hooked prickles common on the young cane, not gland-tipped; prickles on the petioles near the tip of the young cane few, usually 10 to 15 in number, not gland-tipped, 1.5-2.0 mm. in length; petiole glabrous; pedicel and calyx finely tomentose with occasional sessile glands; prickles common on the pedicel and occasional on the calyx; fruit broadly-round, midseason, large, firm, dull purple-red; drupelets large.................... **COLUMBIAN**

BB. Prickles not present on calyx.

C. Leaves at tip of cane tinted with red.

Canes very spreading, almost trailing, very glaucous, with many very small sessile glands; hooked prickles common on the young cane, not gland-tipped; prickles on the petiole near the tip of the young cane common, usually 10 to 15 in number, not gland-tipped, 2.0-3.0 mm. in length; petiole glabrous; pedicel and calyx finely tomentose, with occasional sessile glands, prickles common on the pedicel and absent on the calyx; fruit round, midseason, medium to large, firm, glossy black, without bloom; drupelets rather small.................... **OLDER**

CC. Leaves at tip of cane not tinted with red.

Canes tall, recurving, very glaucous, with many very small sessile glands; straight or slightly hooked prickles common on the young cane, not gland-tipped; prickles on the petioles near the tip of the young cane few, usually 5 to 10 in number, not gland-tipped, 1.0-2.0 mm. in length; petiole glabrous; pedicel and calyx finely tomentose with occasional sessile glands; prickles common on the pedicel and absent on the calyx; fruit conical, early midseason, large, firm, jet black, heavily glaucous; drupelets large .... **CUMBERLAND**

SUMMARY

Nearly all red raspberries cultivated for their fruit in North America have been developed from the American red raspberry *R. strigosus* Michx. and from hybrids between this species and the European red raspberry *R. idaeus* Linn. Many of the botanical characters which separate these two species can be used in the identification of horticultural varieties.

The most useful characters for varietal identification are found to be the presence or absence of glands on the petiole, peduncle, pedicel, and calyx, and whether these glands are stalked or sessile; the form of the leaflets on the young canes, especially the width of the terminal leaflet in relation to its length; the character and abundance of bristles or prickles on the young cane, petiole, peduncle, pedicel, and calyx, especially their abundance on the petiole and the color at their base; the character of the fruit.

A key to 16 varieties of red, black, and purple raspberries is included. This key is based, in so far as possible, on cane and foliage characters so that identification can be made at any time during the growing season.

GLOSSARY

Bristle	Botanically the same as a prickle. Used to designate the typical straight, stiff, bristle-like prickle of the red raspberry
Calyx	The outer floral envelope, consisting of sepals
Drupelet	A small fleshy fruit with a pit or stone. The fruit of a raspberry is composed of an aggregation of drupelets
Epidermis	The outer layer, the skin of plants
Glabrate	Becoming nearly or quite smooth by the loss of pubescence
Glabrous	Smooth, i.e., without hairs or any form of pubescence
Gland	A surface or structure that produces nectar, resin, oil, etc.
Glandular	Bearing glands
Glaucous	Covered with a bloom, a bluish or whitish wax coating
Hypanthium	The cup-shaped structure that bears the sepals, petals, and stamens
Inflorescence	A flower cluster
Pedicel	The stalk of a single flower
Peduncle	The stalk of a flower cluster or of a solitary flower
Petiole	The stalk of a leaf
Pistil	The seed-bearing organ of the flower
Prickle	A sharp, needle-like outgrowth of the epidermis
Pubescent	Hairy
Receptacle	The end of a flower stalk bearing the flower parts
Rugose	Wrinkled, roughened
Sepal	One of the outer cycle of flower parts, usually green, a division of the calyx
Sessile	Without a stalk, seated
Stamen	The part of the flower that bears the pollen
Stigma	The portion of the pistil that receives the pollen
Style	The stalk-like portion of the pistil connecting the stigma and the ovary
Tomentose	Having a dense mat or covering of hairs

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Studies on the Nature of Physiologic Resistance to Puccinia Graminis Tritici

Walter N. Ezekiel

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CONTENTS

Page

Introduction 3

History 4

Present investigations 6

- Material and methods 6
- Characteristics of physiologic forms of Puccinia spp. in hanging-drop cultures 8
  - Germination 10
  - Length of germ tubes 10
  - Length of branches and branching ratios 18
  - Apical swellings on germ tubes 18
- Puccinia graminis tritici in extracts from host plants 26
  - Experiment 1 27
  - Experiment 2 38
  - Experiment 3 40
  - Normal and diseased host tissues as sources of extracts 43
  - Some characteristics of differentiating materials in extracts 49
- Tests of the production of toxins by rust sporelings 53
  - Hypodermic injection of culture filtrates 54
- Absorption of Culture Filtrates 54

Discussion 55

Summary 59

Literature cited 60

STUDIES ON THE NATURE OF PHYSIOLOGIC RESISTANCE TO PUCCINIA GRAMINIS TRITICI[1]

WALTER N. EZEKIEL

INTRODUCTION

The cause of the resistance or the susceptibility of plants to the various Uredinales attacking them has been extensively investigated. Such investigations have been handicapped by the fact that rust fungi have not been successfully cultivated under artificial conditions; and for this reason research in this field in recent years has been limited largely to indirect, cytologic study of the processes involved.

The Uredinales include very highly specialized parasites. Within the species *Puccinia graminis tritici,* numerous physiologic forms have been discovered by Stakman and Levine (30). These forms are identified by their pathologic effect on varieties of *Triticum* spp. The differences by which these forms are distinguished are of a definite qualitative nature. The physiologic forms are classified merely by the type of infection produced. Thus, among the characteristics by which forms 18 and 19 are identified are differences in the reactions of Kanred wheat, C. I. No. 5146,[2] and Mindum, C. I. No. 5296. Kanred seedlings are susceptible to *P. graminis tritici* form 18, that is, however many or few rust pustules develop, there are large uredinia which often coalesce, and there are no hypersensitive areas on the leaves. Kanred seedlings inoculated with form 19, on the other hand, are immune or resistant; there may be no macroscopic evidence of infection at all or there may be hypersensitive or necrotic areas surrounding minute, isolated uredinia. Precisely the opposite is true of the variety Mindum, which is resistant to form 18 and susceptible to form 19. These are not the only differences between forms 18 and 19. Of the twelve wheat varieties used by Stakman and Levine to differentiate physiologic forms of *P. graminis tritici,* only seven react in approximately the same way to both forms. The complexity of the relation existing between the wheat plant and the parasite is evidenced by the fact that on the basis of inoculation tests on only twelve differential wheat varieties more than fifty physiologic forms within *P. graminis tritici* have already been discovered by Stakman, Levine, and their associates.

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[1] Report of investigations pursued under a National Research Fellowship in Botany at the University of Minnesota Agricultural Experiment Station, 1925-27. The writer takes pleasure in expressing his appreciation of the facilities made available by the Division of Plant Pathology and Botany and the Division of Agricultural Biochemistry; of the advice and encouragement of Dr. E. C. Stakman, Dr. R. A. Gortner, and virtually all the members of both divisions; and of the courtesy of E. C. Stakman, M. N. Levine, J. M. Wallace, H. E. Parson, R. U. Cotter, and S. J. Wellensiek in furnishing him with the identified physiologic forms of the various rusts with which they were working. He is particularly indebted for the use of unpublished data with regard to the hosts of new and undescribed physiologic forms, investigated co-operatively by the office of cereal crops and diseases of the United States Department of Agriculture and the Minnesota Agricultural Experiment Station. This manuscript was submitted for publication in April, 1929.

[2] C. I. = Office of Cereal Investigations, United States Department of Agriculture, accession number.

As was pointed out in a summary paper by Zimmermann (35), the relation is so complex that no single, common factor, such as the hydrogen-ion concentration of plants, for instance, could furnish an adequate explanation for physiologic resistance to the rusts. Physiologic resistance might, however, be the result of a complex series of simultaneous gradations in a number of common factors in the host plants, or of differences in specific materials, such as proteins, in different varieties and species. These differences might be assumed to be innate in the host tissues, or again, produced only following the stimulus of infection. The latter assumption, that vegetative growth of Uredinales is dependent on materials produced only in susceptible host cells and only after infection, would explain also the difficulty of growing rusts in artificial culture.

Whatever the immediate cause of physiologic resistance to rusts, it seemed to the writer that it should be possible to find some clue to it by studying the growth of different physiologic forms of rust fungi in extracts from plants susceptible or resistant to them. Such studies have been carried out with physiologic forms of *P. graminis tritici* and extracts of wheat varieties.

The investigations reported herewith were made with the dual aim of obtaining more direct information on the nature of resistance to rusts by a study of the growth of the parasites in extracts from host plants and on other substrata, and of attempting to develop methods of artificial culture applicable to Uredinales. Results relating to the first problem are considered in the present paper.

HISTORY

An elaborate summary of literature on the relation of Uredinales to their host plants is available in Zimmermann's monographic paper (35), and discussion with special reference to the cytologic results in papers by Allen (1, 2, 3, 4), Rice (25), and Wellensiek (34). Only papers of direct interest to the present work will be mentioned here.

Ward (33), Stakman (28), and others showed that the germ tubes of rust fungi may penetrate normally even into immune plants but usually die soon afterward. Resistance in this case thus appeared to be "physiologic"—the result of interaction of the host and the parasite—rather than the result of such morphologic differences as might be concerned, for instance, in mechanical barring of infection by impenetrable epidermis or stomata. Hence the obvious experimental mode of attack on the problem of resistance was to grow rusts on extracts from susceptible and resistant plants and observe the differences; but this was apparently prohibited by the failure of efforts to grow Uredinales successfully in artificial culture. Few records of attempts in this direction are to be found in the literature, and the negative results of Ward (33) are doubtless typical also of other experiments that were unsuccessful and unrecorded.

Ward (33, p. 261) wished to "test the possibility of the leaf containing some body in the cell-sap which inhibits or promotes the growth of the fungus; and I did so by making a cold-water extract of the pounded fresh leaves, rapidly filtering through a stone or other filter, and sowing the spores in the liquid both raw and boiled. In all cases control sowings were made in water, and only those results regarded where the controls showed the spores to be vigorous.

"All attempts of this kind were in vain, however, since vigorous spores germinated equally well in extracts of the leaves of their own host-species and of their antagonistic host species. . . . The positive results do show, however, that the failure of spores from *B. mollis* . . . . to develop pustules on *B. sterilis,* for instance, is not due to a mere exudation of some antagonistic soluble extract—that the antagonism must be due to something far more subtle than a mere soluble poison oozing from the cells."

Leach (17) tried to determine the possibility of toxin or antitoxin formation following invasion. He germinated urediniospores of *P. graminis tritici* in extracts from normal and inoculated wheat seedlings, but was unable to correlate variations in the percentage of germination and the length of germ tubes with the resistance of the host from which the extract was made. He suggested, however, that rust resistance might be due to specific nutrient requirements of rusts, which would be satisfied only in congenial host plants.

Attempts have been made to correlate physicochemical properties of host plants with their resistance to rusts. Comes (7) suggested that the acidity of the cell sap was the property that enabled wheat plants to resist rusts. Miss Hurd, however, could not correlate the hydrogen-ion concentration of the expressed juice of normal wheat plants of different varieties with their relative susceptibility to stem rust (13), nor the changing acidity of different stages of wheat growth (14) with any variations in susceptibility to rust during the development of the plant.

Hursh (15) found that urediniospores of some physiologic forms of *P. graminis tritici* appeared to germinate at slightly different ranges of temperature and acidity. He was, however, unable to correlate physicochemical properties of juice from normal wheat plants of different varieties with their resistance to rust (16).

Definite morphologic resistance has been shown to exist in the case of two stages of stem rust. Hursh (16) found that the mycelium of *P. graminis* is restricted in wheat stems to the collenchyma tissue, and thus explained the slight injury in varieties with little collenchyma tissue as due to this mechanical limitation of the spread of the mycelium. He emphasized, however, that this morphologic resistance was concerned only in determining the amount of damage that might occur in different varieties, and that "the differences in the reaction of wheat varieties to different biologic forms of *P. graminis tritici* appear to be due entirely to physiologic causes."

Melander and Craigie (21) have studied the nature of resistance of species of *Berberis* to *P. graminis*. They found that species with epidermis resistant to puncture were usually resistant to infection also. However, the reverse was not true in all cases, and they conclude that there probably is physiologic resistance also.

PRESENT INVESTIGATIONS

Material and Methods

All wheat varieties used were of the particular selections employed by Stakman and Levine (30) as differential hosts in the determination of physiologic forms of *P. graminis tritici*. Plants grown in the greenhouse were in five-inch pots of steam-sterilized soil. In the field, plants were drilled in rod rows as required. Greenhouse plants were grown on benches or in compartments that guarded against possible accidental rust infection, while field-grown material was exposed to natural infection.

In the preparation of extracts, plants were cut about one-half inch above the ground. The entire aerial portion was used, except noticeably dried or mechanically injured leaf tips, which were trimmed off. Grinding, when employed, was done in an ordinary meat grinder. The press cups used in the hydraulic press were of non-corrosive "Monel" metal. Small Berkefeld or Mandler diatomaceous filters of the coarser type (requiring only about five pounds of air pressure to force air bubbles through the thoroly wet filter cylinders) were used for ultrafiltration of plant extracts.

Materials to be used as substrata, including sterile distilled water, were stored in Pyrex tubes and flasks in the refrigerator. They were handled in sterile pipettes, with the usual aseptic precautions, in preparing dilutions from the concentrated materials.

Agar was the diluent for the plant extracts of some series. In preparing cultures in these series, the melted agar was cooled to 45°

C. before the required amount of extract was added, and held at this temperature while drops were removed.

Since observations were made of microscopic differences, hanging-drop cultures were employed almost exclusively. The substrata tested were therefore in contact only with cover-slips during the experiments. New cover-slips were used and cleaned as follows: autoclaved in cleaning solution, rinsed in distilled water, scrubbed with a camel's-hair brush under a stream of distilled water, rinsed and stored in alcohol. Glass rings and slides were also specially cleaned, stored in alcohol, and flamed off immediately before use. Rings were sealed to the slides with paraffin and to the coverslips with vaseline in the customary way. Hanging drops, of either liquid or melted agar substrata, were made with a needle loop of 4-mm. diameter; and this loop was not only sterilized but also washed between successive drops. No liquid was used at the bottoms of the cells.

Identified physiologic forms of the various rusts under investigation in the Division of Plant Pathology and Botany of the Minnesota Agricultural Experiment Station were available for inoculum. Most use was made of the forms of *P. graminis tritici* as identified by Stakman and Levine (30); and only a few cultures of *P. graminis avenae, P. graminis secalis, P. coronata,* and *P. sorghi* have been studied. Usually only one strain of a given physiologic form was studied. The accession numbers of the particular strains of *P. graminis tritici* used in this work are listed in Table IV.

Growth was studied from urediniospore inoculation only. Inoculum was taken from inoculated plants, usually grown in pots in the greenhouse, but occasionally in large culture tubes. In either case, inoculum to be used in a given series was collected from plants of approximately the same age and at the same period of rust development. Little Club wheat, C. I. No. 4066, is susceptible to almost all of the forms of wheat stem rust studied and was used to develop inoculum in most cases. *P. graminis tritici* forms 18 and 19, which were studied most extensively, were carried along on Little Club plants in neighboring wards in the greenhouse, separated only by a sheet of glass; and were periodically transferred at the same time to new plants, to furnish inoculum as uniform as possible.

For inoculation of cultures, urediniospores were taken from a number of pustules on different leaves and mixed in a dry, sterile Petri dish by stirring with a straight needle. A thin needle with a bent tip was run through this comparatively uniform mixture of spores, tapped lightly against the dish a definite number of times to remove most of the adherent spores and give a more regular number of spores per load, and then used to inoculate both of a pair of drop cultures. An inoculum of 50-150 spores per drop was customarily used except when the density of inoculum was a variable of the experiment. In the case of liquid drops, the spores were distributed quite evenly throughout the drops by vigorous stirring with the needle. In agar drops, spores were distributed by touching the needle very lightly to the surface of the drop at a number of points in rapid succession, and the spores here were present in groups at some points in each drop and singly at other points.

During the whole investigation, all cultures were incubated in the dark at 20° C. or within about one degree of this temperature. Growth was usually complete in about 17 hours and measurements were made from 19 to 23 hours after inoculation. These were checked by final observations again in three days to a week, and the slight additional growth noted on rare occasions was added to the first figures. The results presented below are then the total growth obtained in various substrata under the conditions of the experiment rather than the growth within any specified time.

Observations were made on the living, unstained material. In most experiments the notes included counts of the number of spores in the drop, counts or estimates of the germination, codified notes on the general type of growth occurring, and measurements of 10 sporelings selected at random in different parts of the drop. As all cultures were run in duplicate, there were 20 sets of measurements for each dilution of each substratum tested. This appeared to be a fairly representative sample of the cultures, but further accuracy could have been obtained by additional replication. Growth was measured only in the case of spores sufficiently separated from others in the drop so that it could be seen that no fusion of adjacent sporelings had occurred; as when this happens the resulting growth may be much longer than that from a single spore. Measurements were made of the length of the main germ tube, and of the total length of all branches. Coiling, circumnutatory growth is frequent in urediniospore germ tubes and these measurements were partly estimates of the lengths of such curved portions. However, their reliability was indicated by the close agreement of successive sets of measurements in the same cultures. The same microscope and ocular micrometer were used throughout the investigation.

Characteristics of Physiologic Forms of Puccinia Spp. in Hanging-Drop Cultures

The varieties and physiologic forms of *P. graminis* were originally differentiated only by the reactions of the various host plants. Stakman and Levine (29, 18) have pointed out consistent differences in color, shape, and size of urediniospores of varieties of *P. graminis;* and Levine (19) demonstrated distinct differences between urediniospores of physiologic forms within *P. graminis tritici.* Physiologic differences between these forms were noted by Hursh (15) in his studies of the relation of temperature and hydrogen-ion concentration to the germination of urediniospores.

In the work with hanging-drop cultures reported herein, the writer has found additional and readily demonstrable differences between the physiologic forms included. Growth was studied from about 200,000 urediniospores, and was measured for about 22,000 of the sporelings obtained. In very few of the cultures was the growth obtained much greater than that shown by Sappin-Trouffy (26), Plowright (23), and others. It was found that even this slight growth, extending usually less than 1000 μ and reaching its maximum development in less than 24 hours, showed definite, constant characteristics which differed not only for urediniospores of the same physiologic form on different media, but also for germ tubes of different physiologic forms grown under identical cultural conditions.

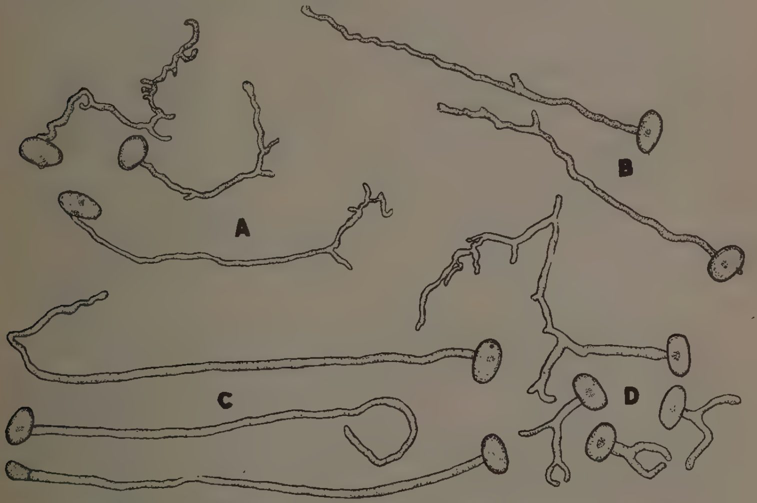

Fig. 1. Growth from Urediniospores of *P. graminis tritici* Physiologic Forms 18 and 19
A, form 19, and B, form 18; in sterile, distilled water, 25 hours. C, form 18 and D, form 19; in extract from normal Kanred plants, centrifuged and ultrafiltered (Table XXII) and diluted to 0.01 with sterile, distilled water, 2 days. Outlined with camera lucida, × 200.

Typical sporelings of form 18 and form 19, shown in Figure 1, A and B, illustrate differences characteristic of the growth of these forms in many substrata. The germ tubes of form 18 are longer than those of form 19, are coiling, and have few branches which, if present, are usually toward the tip. On the other hand, germ tubes of form 19 are shorter and rarely coiling, and have many branches which arise dichotomously at intervals along the entire germ tube and give it a scorpioid appearance.

Differences between germ tubes of the various physiologic forms are both qualitative and quantitative. The length of germ tubes, length of branches, and abundance of apical swellings are characteristics which were conveniently recorded quantitatively. These were considered fully in study of the results.

Other prominent differences are more of a descriptive nature and are not readily recorded quantitatively. For example, germ tubes may develop in a coiling or circumnutatory manner or remain quite straight; branching may be simple or dichotomous; and branches may be distributed along the germ tubes or localized near the tip or the base. Such differences have been observed, together with numerous gradations and combinations of them. Some of these differences are measurable, but summation or averaging of the measurements would hardly be valid and comparison of them would be difficult. These more qualitative differences have therefore been ignored in summarizing these studies.

Germination

Urediniospores of *P. graminis* have a number of germ pores, usually four, arranged equatorially. When the spores are placed in water, growth starts usually from two or more of the germ pores. There is apparently a strong "apical dominance" in the growth of the germ tubes, however, and only one germ tube develops to any considerable length.

In the laboratory the percentage of germination of urediniospores is frequently nearly 100 per cent in distilled water. The percentage of germination is not a good criterion for the comparison of substrata from this angle, as higher percentages would be impossible. The writer has found also that the percentage of germination may vary more with the age or methods of handling the urediniospores than do the characteristics of the germ tubes produced from these spores. In the present study the percentage of germination has accordingly been considered only in occasional experiments.

Length of Germ Tubes

As used in the present paper, "length of germ tube" is considered the length of the mycelium from the spore to the tip, or if a side branch was longer than that which seemed to be the main germ tube, to the tip of this branch. Length of germ tubes varies widely with changes in the environmental conditions, and, as shown below, even with the number of spores with which a drop is seeded. Variations according to environment are not necessarily the same for different physiologic forms of the same species. Thus, on one substratum germ tubes of a form may average distinctly longer than those of another, while on a different substratum the relation may be just the reverse. Hence differences between physiologic forms based on lengths of germ tubes apply only for conditions specified.

This is demonstrated well in Table I with forms 18 and 19 of *P. graminis tritici.* In both sets of cultures on plain, one per cent agar, germ tubes of form 18 were nearly twice as long as those of form 19. In the dilute Shive's solution agar, however, germ tubes of form 19 invariably averaged longer than those of form 18. This relation between the growth of these two physiologic forms on plain agar and on Shive's agar was constant not only for the series listed in Table I but also in numerous experiments in which these physiologic forms were used repeatedly as checks in plain agar and Shive's agar.

TABLE I

EFFECT OF DIFFERENCES IN THE SOURCE OF INOCULUM AND OF CULTURE MEDIA ON THE CHARACTERISTICS OF PHYSIOLOGIC FORMS OF *P. graminis tritici* IN HANGING-DROP CULTURES, IN DUPLICATE AT 21° C.

Sources of inoculum	Substrata	Physiologic forms of *P. graminis tritici*	Mean lengths of germ tubes, in microns	Ratio, lengths of branches over lengths of germ tubes	Relative abundance of apical swellings†
Plants inoculated 36 days previously; pustules old	Plain 1% agar	18	310	0	+ +
		19	160	.174	?
	Dilute Shive's agar*	18	157	.109	+
		19	256	.147	?
Plants inoculated 15 days previously; pustules still fresh	Plain 1% agar	18	403	.008	+ +
		19	260	.120	+
	Dilute Shive's agar*	18	208	.098	?
		19	241	.206	—

* Shive's "best" solution (20) diluted to 0.1 concentration in one per cent agar.

† + + = numerous apical swellings; + = few; ? = doubtful; — = none.

Relation of density of inoculum to length of germ tubes.—All the various substrata tested, including the checks in sterile distilled water or plain agar, were run in duplicate for each physiologic form in each experiment. The average lengths of germ tubes producd in such duplicates were rarely closely similar. It was soon noted that germ tubes seemed to be longer in the drop that had been seeded with the greater number of urediniospores. Some variation between duplicates was to be expected, but the possibility that much of this variation might be due directly to differences in the density of inoculum made it desirable to study the relation of this factor to growth.

The results in distilled-water check cultures, from various experiments, were first considered. The relation between the number of spores per drop and the mean lengths of germ tubes obtained is shown in Figure 2 for such a collected series of cultures of form 18, and in Figure 3 for form 19. In both cases a definite positive correlation is evident between the number of spores present per drop and the mean length of germ tubes produced. The correlation is + .49 ± .09 for form 19 and + .43 ± .09 for form 18. These correlations may be interpreted as indicating that with form 18 approximately 18 per cent, and with form 19 approximately 24 per cent, of the total variation in lengths of germ tubes shown in the graphs can be explained by differences in the density of inoculum.

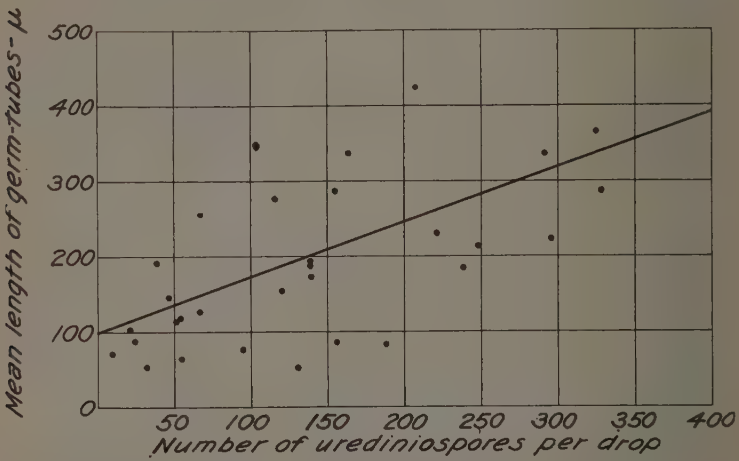

Fig. 2. Correlation of Number of Urediniospores of Physiologic Form 18, *P. graminis tritici*, per Drop of Sterile, Distilled Water, with the Mean Length of Germ Tubes Produced. r = + .427 ± .090

It is to be remembered that the individuals of these series were not directly comparable, as they were merely check cultures picked out from series of cultures during a period of nearly three months. Variation owing to differences in the inoculum used (tho of the same strains of rust and from the same host plant, differing at times as to age of the pustule from which it was taken, seasonal differences in greenhouse conditions under which sporulation occurred, etc.), as well as possible slight differences in the cultural conditions, was to be expected. The true correlations here are doubtless considerably higher.

Data secured with other forms tended to confirm the validity of this relation. Some cultures of *P. graminis tritici* forms 1 and 14 were seeded at varying rates, all in hanging drops of Shive's "best" solution (20) diluted to 0.1 in distilled water and adjusted to pH 3.2 with N/100 HCl.

In 7 cultures of form 1, the mean lengths of germ tubes varied almost directly with the amount of inoculum (Fig. 4), from 45 μ in a culture with 15 spores to 597 μ in one with about 2,100 spores. The correlation for the series was + .93 ± .033. With the 16 cultures of form 14 (Fig. 5) a mean length of germ tubes of 128 μ was produced in drops containing 50 urediniospores, while in a drop containing 670 spores the mean length was 420 μ. For this form the correlation was + .95 ± .018.

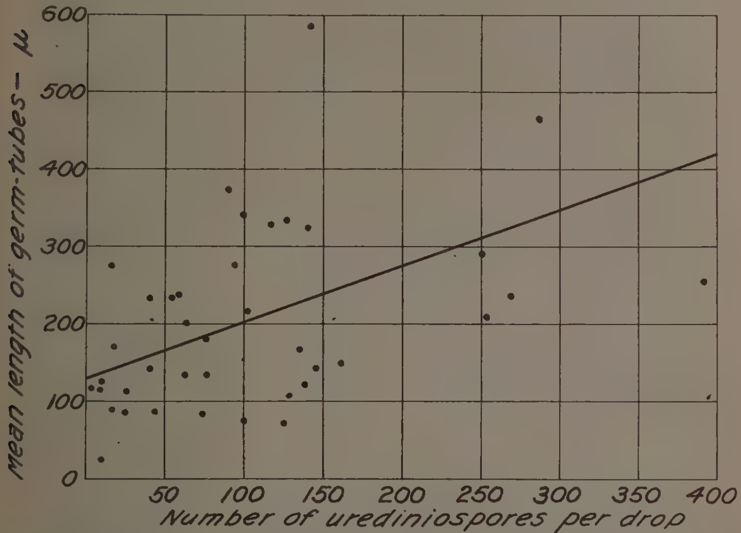

Fig. 3. Correlation of the Number of Urediniospores of Physiologic Form 19, *P. graminis tritici*, per Drop of Sterile, Distilled Water, with the Mean Length of Germ Tubes Produced. r = + .492 ± .090

Whatever the cause of this increase of growth with increase of density of inoculum, the fact that it does occur appears unquestionable. Also, since it is impracticable to set up extensive experiments of this kind with a very carefully controlled number of spores in each drop, results of growth in various substrata should be corrected for this factor before they are strictly comparable, if small differences are to be significant. Such a correction has been used at times with forms 18 and 19 on the basis of the data shown in Figures 2 and 3. The regression formulae calculated from these figures were possibly better for this purpose because of the fact that the data concerned were composites of many series; and the mean check values calculated were perhaps more truly representative than if they had been based on the results of single series.

Values were calculated along the regression lines for cultures of forms 18 and 19, respectively, at each change of five spores per drop. This furnished estimated "check" cultures with densities of inoculum corresponding to those of any cultures that might be considered. Such estimated check values were usually subtracted from the average length of germ tubes obtained experimentally in the media tested, thus eliminating density of inoculum as a variable factor. The results were considered "net increases," either positive or negative, in length of germ tubes for the particular substrata used in the experiment as compared to growth in sterile, distilled water. As a matter of fact, however, this interpretation is not always quite correct. It presupposes that the rate of increase with density of inoculum will be the same in each substratum tested as it is in water, which is probably not true. This rate appears to be lower in most substrata than it is in distilled water.

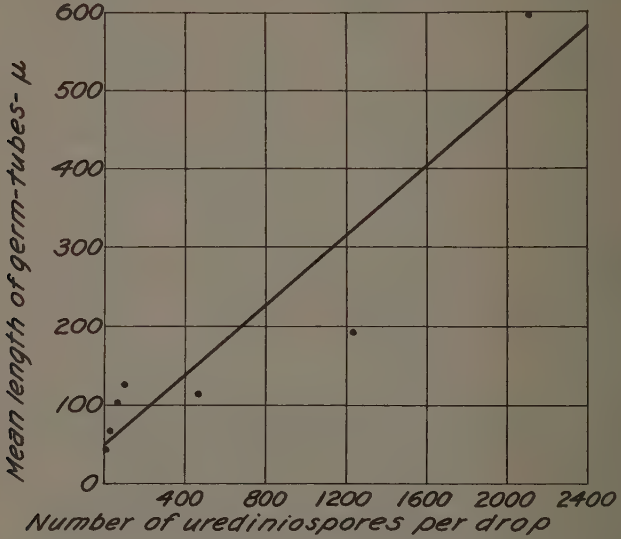

Fig. 4. Correlation of the Number of Urediniospores of *P. graminis tritici* Physiologic Form 1, per Drop of Diluted Shive's Solution, with the Mean Length of Germ Tubes Produced. $r = + .933 \pm .033$

To minimize error, therefore, the amount of inoculum has been kept as nearly constant as possible, even tho a correction for density of inoculum could be applied. In any case, use of the estimated check values has furnished a method of showing that observed results in tests of substrata are probably due to the factors under examination rather than to variations in density of inoculum. Application of the correction formulae to substrata other than distilled water probably over-corrects for differences in density of inoculum; and experimental results would appear unimpeachable from this angle when the same relation is shown, whether or not the estimated check values have been used.

Density of inoculum and length of germ tubes in agar drops.—The correlations shown above were of growth in liquid substrata. Many other series were run in which the nutrients were diluted in one per cent agar. While the density of inoculum did not appear so important here as in liquid media, it seemed desirable to ascertain whether it needed to be considered as a factor.

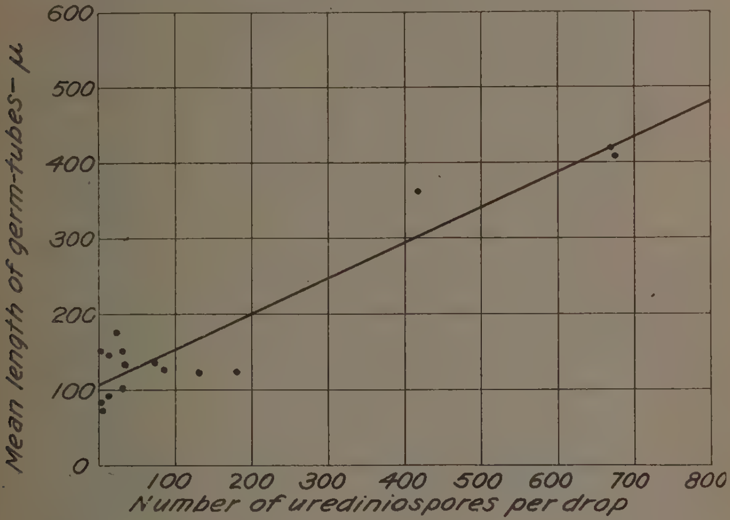

Fig. 5. Correlation of the Number of Urediniospores of *P. graminis tritici* Physiologic Form 14, per Drop of Diluted Shive's Solution, with the Mean Length of Germ Tubes Produced. r = + .945 ± .018

Forms 1, 18, and 19 of *P. graminis tritici* were seeded at varying rates in hanging drops of plain, one per cent agar. The results confirmed those previously obtained. The length of the germ tubes of each form increased with increased density of inoculum (Fig. 6). On the agar, however, growth was relatively greater at the lower concentrations of inoculum than in liquid substrata. In the latter, the regression lines, showing the best estimated values of lengths of germ tubes on the basis of density of inoculum, tend to approach zero as the density of inoculum decreases. In the agar cultures, on the contrary, with even fewer than 10 spores in a drop, the germ tubes usually averaged more than 200 μ in length.

Further correlations of growth with density of inoculum have been made, using assembled data of the growth in plain, one per cent agar drop cultures that were run from time to time as checks for different series. The results, along with the three correlations discussed above, are given in Table II.

Decided positive correlation may be noted in the case of each rust form used. The coefficients of correlation, as might be expected, are higher in series in which there were fewer cultures. The regression equations in the last column of Table II give the method by which probable values can be assigned to lengths of germ tubes on the basis of the number of spores per drop. In these equations the constants by which "A" (the number of spores) is multiplied express the rate at which increase in number of spores increases length of germ tubes; while the second constant of each equation is the estimated length of germ tubes with "o" spores per drop, and is added to the first product to obtain the actual length in microns. Both of these constants varied with the different forms. There appears little reason to doubt that variation of this sort actually exists between physiologic forms of *P.*

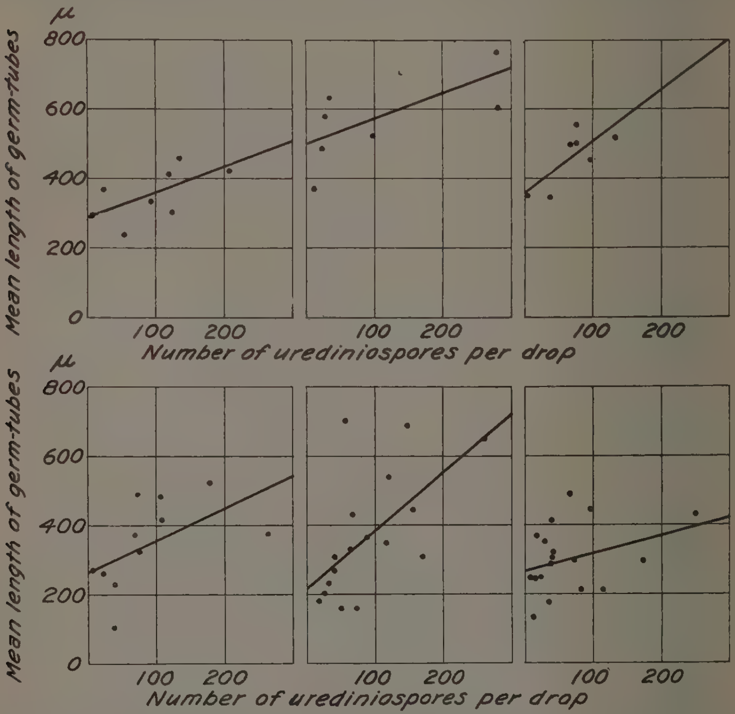

Fig. 6. Correlation of the Number of Urediniospores per Drop of Plain One Per Cent Agar with the Mean Length of Germ Tubes Produced

Left to right, physiologic forms 1, 18, and 19. Upper row based on results from single series, lower row on assembled data from several series. Coefficients of correlation in Table II.

TABLE II

SUMMARY OF CORRELATIONS OF THE NUMBER OF UREDINIOSPORES PER DROP AND THE MEAN LENGTH OF GERM TUBES PRODUCED, IN ONE PER CENT PLAIN AGAR HANGING-DROP CULTURES

Physiologic forms of *P. graminis tritici*	No. of cultures per series	Coefficients of correlation	Regression equations*	
1†	11	+ .547 ± .142	$X = .922A + 268$	$.825A + 277$
1‡	8	+ .646 ± .139	$X = .728A + 285$	
9†	8	+ .691 ± .124	$X = .895A + 230$	
17†	12	+ .569 ± .132	$X = .456A + 310$	
18†	17	+ .598 ± .105	$X = 1.68\ A + 220$	$1.201A + 360$
18‡	8	+ .658 ± .135	$X = .722A + 500$	
19†	18	+ .339 ± .141	$X = .523A + 272$	$1.024A + 312$
19‡	7	+ .745 ± .113	$X = 1.525A + 352$	
27†	8	+ .687 ± .126	$X = .382A + 217$	
Mean regression value, used later in correction of experimental results for variations in density of inoculum			$X = .87A +$	

* X = estimated lengths of germ tubes, in μ; A ≐ number of spores.

† Assembled data from several series.

‡ Data from a single series.

graminis tritici. It is quite probable, for instance, that both the rate of increase and the characteristic constant to be added are higher for form 18 than for form 19.

On the other hand, equations calculated from single series of cultures grown simultaneously are quite different for each form from those calculated from assembled data of many series. Such variation might be encountered in any series to which these equations might be applied; therefore it has seemed needless to try to use individual equations for the different forms. The equation averaged from those in Table II has been used instead, in correcting results, with any form of *P. graminis tritici,* for differences in density of inoculum in agar drops in the experiments to be considered below.

The results given in Figures 2 to 6 and Table II show that in drop cultures inoculated with urediniospores of *P. graminis tritici* the mean length of germ tubes increases with the density of inoculum. The cause is not yet known, but the following explanation appears probable. Urediniospores contain stored materials which migrate into the germ tubes as growth starts. A portion of these materials may diffuse more or less slowly out of the germ tube into the surrounding substratum. Then, the greater the number of germ tubes in a given drop, the higher will become the concentration of soluble nutrient or stimulating materials in the drop available for absorption by germ tubes. The difference between results in liquid and agar drops is also explained by this hypothesis. Diffusion away from germ tubes in agar would be much slower than in liquid drops; hence, even at the lowest concentration of inoculum, we should expect the relatively long germ tubes which were actually found. Such variation according to density of inoculum as does occur in the agar cultures is probably the result of diffusion of materials in a surface film of water, rather than of diffusion through the agar. While it is probably the area of mycelium present per drop that affects the length attained per germ tube, what was counted (as a matter of convenience) was the total number of spores present. The correlations above might be still higher were they calculated instead from the number of spores that germinated.

Length of Branches and Branching Ratios

The total length of branches of the germ tubes was secured simply by summation of the length of all branches. There is considerable variation in the extent of branching of different physiologic forms, even of the same species. This is shown not only in the length of the branches, but also in the number of branches per germ tube. The number and size of branches is, of course, affected by cultural conditions also.

In comparing branching in different substrata or by different forms it has been convenient to correct for the differences in extent of growth in different media by using a "branching ratio," obtained by dividing the average total length of branches per germ tube by the average length of germ tubes. This ratio is larger than the portion of the total vegetative growth of the young sporeling that consists of branches. Thus, with a germ tube measuring 200 μ and branches totaling the same length, only half of the total growth would consist of branches. The branching ratio (200 divided by 200) would, however, be 1.0. Furthermore, these ratios are based on the extent of branching only, without regard to the number of branches per germ tube that may be included to make up the total length of branches.

Differences in branching ratios of different physiologic forms are relatively constant and have been of value in the comparison of substrata.

Apical Swellings on Germ Tubes

It has been observed previously that the dense spore contents of germinating urediniospores migrate out into the germ tube (Fig. 7, A) and toward its apex. Not infrequently these materials reach the tip of the germ tube, which may then become more or less inflated and appear somewhat sporelike. Such inflations of the tips of rust germ tubes were described by Tulasne (31, p. 152) as early as 1854, and have been noted since by Plowright (23), Büsgen (5), Hitchcock and Carleton (12), Sappin-Trouffy (26), and Spaulding (27). They have been considered generally merely as anomalous growths due to the abnormal conditions of artificial culture.

Apical swellings have been produced, apparently normally, by all the physiologic forms of all species studied during this investigation, tho not necessarily at the same rate in each case. The bodies have been produced on a wide variety of substrata: distilled water, plain agar, Shive's solution, M/1000 dextrose solution, wheat extracts, autolyzed yeast decoctions, etc. They have been seen on sporelings quite isolated from any other growth in the cultures, so that fusion of colonies is not a prerequisite for their production.

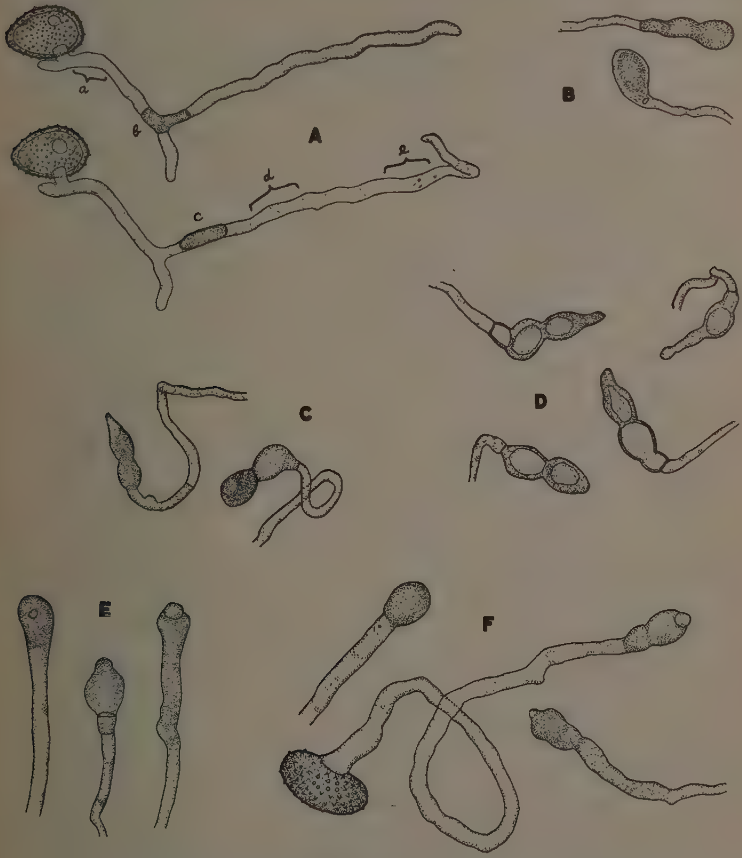

Fig. 7. A, progress of spore contents toward tip of a germ tube of form 1, in an agar hanging-drop culture at room temperature of 21° C. Time since inoculation, *a*, 3 hours; *b*, 3 hours, 45 minutes; *c*, 4 hours; *d*, 5 hours; and *e*, 23 hours.

B to F, apical swellings on tips of germ tubes of *P. graminis tritici* in hanging-drop cultures. B, D, and E, form 1; C, form 14; and F, form 23. Substratum plain one per cent agar, except for D which was in extract from normal Kanred plants diluted in agar to .01. (Table XXVII.) Camera lucida, × 400.

Series of hanging-drop cultures of various physiologic forms of *P. graminis tritici, P. graminis avenae, P. graminis secalis,* and *P. coronata avenae* were grown on plain agar for the express purpose of studying the apical bodies. They were found in cultures of all the rusts mentioned. The swellings usually were spheric to clavate, with dense, brown contents but without definite septation from the germ tube, as shown in Figure 7, F, and Figure 8, A, B, and C. Less frequently these swellings were divided from the germ tube by a well-developed wall, and occasionally the swelling itself was septate as shown in Figure 7, C, D, and E. Typical swellings when first formed were nearly the color of normal urediniospores, and the most highly developed very closely resembled teliospores. In a single case it was observed that the apical swelling on a germ tube of *P. coronata* bore on its tip a number of denticulate outgrowths very similar to those present on normal, mature teliospores of this species.

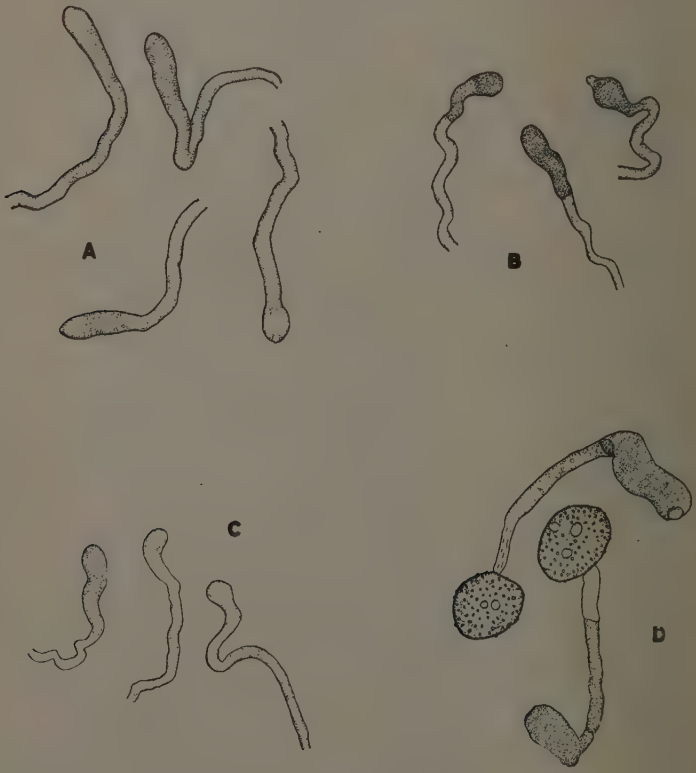

Fig. 8. Apical Swellings in Hanging-Drop Cultures in Plain One Per Cent Agar
A, *P. graminis avenae* form 4 (Acc. No. 8406); B, *P. graminis secalis* form 11 (Acc. No. 1317); C, *P. graminis secalis* (Acc. No. 1374); and D, *P. coronata avenae* (H. E. Parson's Acc. No. 6). Camera lucida, × 400.

No further development of these bodies has been observed. At least in the hanging-drop cultures studied, they appear to reach their fullest development within 24 hours, tho additional septation apparently may occur (or possibly merely becomes more noticeable) up to 36 or 48 hours, after which, gradual degeneration usually starts. The contents of the inflated tip lose the brown color derived from the translocated urediniospore material and become first olivaceous or greenish brown, then densely protoplasmic but hyaline, and later more and more vacuolate. (See Fig. 9, B.)

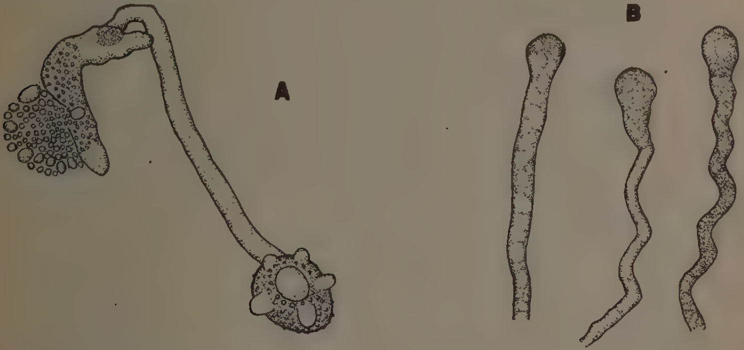

Fig. 9. A, unusual type of degeneration of apical swelling, *P. coronata avenae* (H. E. Parson's Acc. No. 6).

B, usual slow degeneration of apical swellings. *P. graminis tritici* form 29, culture on plain one per cent agar, drawn 15 days after inoculation. Note vacuolation even of the tips of the germ tubes. Outlined with camera lucida, × 400.

Apical swellings on germ tubes of *P. coronata* generally were of a less clearly defined shape than those of *P. graminis tritici.* Those shown in Figure 8, D, are quite representative of certain series. An unusual type of disintegration observed in one case with *P. coronata* is shown in Figure 9, A. This germ tube was in a hanging-drop culture on plain agar, incubated for 17 hours at 21° C. The culture was taken out of the incubator for microscopic examination at room temperature, about 26° C. Just as the swelling shown in Figure 9, A, had been noted, about 20 minutes after the slide was removed from the incubator, the contents apparently exploded the side of the inflated tip. The oily droplets that exuded were brown.

As mentioned above, apical swellings are not produced in the same abundance by different physiologic forms of the same species. For example, they were produced on a much higher percentage of germ tubes of form 18 than of form 19 of *P. graminis tritici,* and this relation held true through many series during a period of two years. Similarly, some physiologic forms of *P. graminis tritici,* such as forms 1 and 23, produced these bodies in profusion, frequently on nearly every germ tube in a series, while other forms produced very few. The rate of production seemed roughly proportional to the abundance of teliospore production by these forms on plants of Little Club wheat in the greenhouse. The production of teliospores by 8 physiologic forms of *P. graminis tritici* on Little Club wheat seedlings that were grown in the greenhouse in large glass tubes on cotton moistened with Shive's solution is recorded in Table III. Notes on tubes in which plants had been inoculated one, two, and three months previously are included; but unfortunately there were only a few plants infected with each physiologic form. In general, the physiologic forms that produced large numbers of apical swellings in artificial culture also produced teliospores abundantly on Little Club plants, which are susceptible to all of the forms included in Table III. There would be much closer correlation here except for the few apical swellings produced by form 27. The apparently aberrant relation of this and other physiologic forms to which Vernal emmer is susceptible will be discussed in some detail later.

TABLE III

COMPARISON OF ABUNDANCE OF TELIOSPORES PRODUCED ON LITTLE CLUB WHEAT SEEDLINGS, GROWN IN GLASS TUBES, WITH THE ABUNDANCE OF APICAL SWELLINGS PRODUCED BY THE SAME PHYSIOLOGIC FORMS OF *P. graminis tritici* IN PLAIN-AGAR HANGING-DROP CULTURES

Physiologic forms of *P. graminis tritici*	Teliospores on Little Club wheat plants	Average percentage of apical swellings on germ tubes in artificial cultures
14	None	5
19	do	6
21	Occasional	29
1	do	47
18	do	22
15*	do	16*
23	Profuse	49
27*	do	11*

* Forms 15 and 27, to which Vernal emmer is susceptible, are aberrant in most classifications of these results.

The evidence at hand on the morphologic resemblance of apical swellings to the teliospore stage of rusts, and on the somewhat low correlation of the rate at which they are produced with the abundance of normal teliospore production on wheat plants, is perhaps insufficient to prove that apical swellings on urediniospore germ tubes are actually immature teliospores. The writer would suggest that this is probably the case, altho conclusive proof is still lacking.

Relation of density of inoculum to production of apical swellings.—Altho the length of germ tubes was affected to a marked degree, both in liquid and agar drops, by the numbers of spores present per drop, there did not appear to be so pronounced an effect of density of inoculum with regard to the percentage of germ tubes that produced apical swellings. In general, the relation seemed to be that the fewer the spores per drop, the more abundant the apical swellings.

Data are given in Figure 10 for the production of apical swellings and the number of spores per drop in a collected series of cultures of *P. graminis tritici* form 1 in plain agar. The correlation here is low (— .253 ± .145) but still plainly negative.

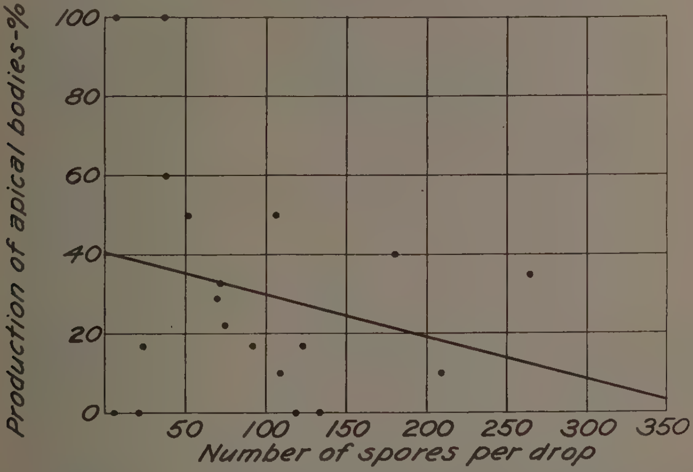

Fig. 10. Correlation of the Percentages of Germ Tubes Producing Apical Swellings, in Plain-Agar Drop Cultures of *P. graminis tritici* Form 1, with the Numbers of Spores per Drop. $r = -.253 \pm .145$

Corrections in results of experiments in which the amount of inoculum varied were occasionally made on the basis of the regression line shown in Figure 10, thus using the regression equation with form 1 as a general one to apply to all physiologic forms of *P. graminis tritici* on plain agar. This usage is not quantitatively correct but has probably not introduced any important error into the results.

The relation here was to be expected, in that increased density of inoculum had an effect on the production of apical swellings opposite to that found for the length of the germ tube. Germ tube elongation rather clearly represents vegetative growth, while the apical swelling appears to indicate a tendency toward reproduction, even if abortive. It is possible that germinating urediniospores, almost irrespective of environment, tend to enter a resting stage quickly, and transfer their contents into teliospores, unless some rather specific conditions inhibit reproduction and permit vegetative development.

Relation of production of apical swellings to the host range of physiologic forms.—There were marked differences between physiologic forms with respect to the percentage of germ tubes that produced apical swellings. The question arose as to the physiologic significance, if any, of these differences.

Parson (22) had noted considerable differences in the readiness with which physiologic forms of *P. coronata avenae* produced telia on host plants, and concluded that "it seems likely that there is a correlation between the narrow pathogenic specialization of a strain and early formation of telia, but this cannot yet be stated with certainty." Since it was suspected that the apical swellings produced on urediniospore germ tubes were immature teliospores, the possibility that the rate of production of these bodies also might be associated with the narrowness of the host range was investigated.

The average percentages of apical swellings produced by germ tubes of 19 physiologic forms of *P. graminis tritici* are listed in Table IV and shown graphically in Figure 11. The percentages are fairly accurate; enough cultures of most physiologic forms were grown so that the average percentages were changed only slightly when results from individual cultures were corrected for variations in density of inoculum. There were 7 physiologic forms to which more than 5 of the 12 wheat varieties are resistant. Apical swellings were produced on more than 30 per cent of the germ tubes of all but one of these

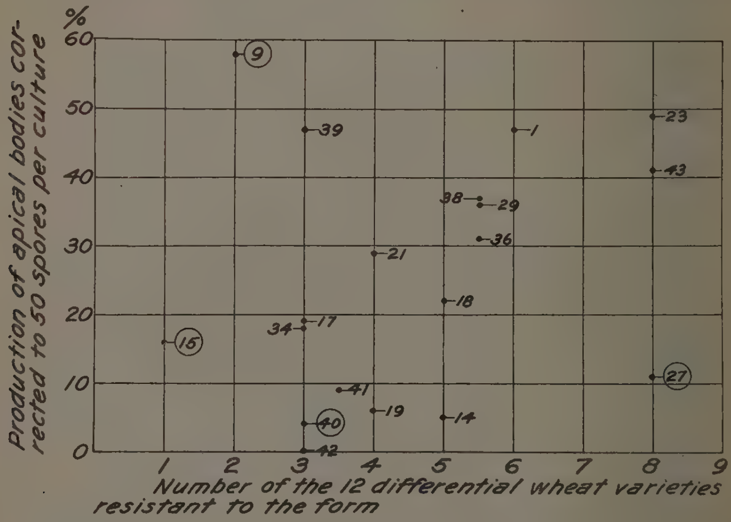

Fig. 11. Relation of the Mean Production of Apical Swellings by Physiologic Forms of *P. graminis tritici* in Plain One Per Cent Agar Hanging-Drop Cultures, to the Host Ranges of These Forms

Forms to which Vernal emmer is susceptible are shown in circles. Omitting these forms and form 39, r = + .791 ± .067.

forms. On the other hand, there were 12 physiologic forms to which 5 or fewer wheat varieties are resistant. Apical swellings were produced on less than 30 per cent of the germ tubes of all but two of these forms. In other words, physiologic forms of *P. graminis tritici* with relatively restricted host ranges usually produced more apical bodies than those forms with wider host ranges.

TABLE IV

PERCENTAGE OF APICAL SWELLINGS ON UREDINIOSPORE GERM TUBES OF PHYSIOLOGIC FORMS OF *P. graminis tritici* IN PLAIN, ONE PER CENT AGAR HANGING-DROP CULTURES, AND HOST RANGES OF THE FORMS

Physiologic forms of *P. graminis tritici**	Host range. No. of the 12 differential wheat varieties resistant to the form	Percentage of germ tubes producing apical swellings, corrected to 50 spores per drop
1 (Acc. No. 2)	6	47
9 (Acc. No. 1576)	2	58
14 (Acc. No. 581)	5	5
15 (Acc. No. 849)	1	16
17 (Acc. No. 1312)	3	19
18 (Acc. No. 957)	5	22
19 (Acc. No. 1297)	4	6
21 (Acc. No. 1497)	4	29
23 (Acc. No. 1281)	8	49
27 (Acc. No. 846-c)	8	11
29 (Acc. No. 738)	5.5†	36
34 (Acc. No. 1575)	3	18
36 (Acc. No. 1097)	5.5†	31
38 (Acc. No. 794-b)	5.5†	37
39 (Acc. No. 1163)	3	46
39 (Acc. No. 1605)	3	48
40 (Acc. No. 1010-e 2)	3	4
41 (Acc. No. 1010-f)	3.5†	9
42 (Acc. No. 1010-i)	3	0
43 (Acc. No. 1569)	8	41

* Numbers in parentheses are University of Minnesota, Division of Plant Pathology and Botany accession numbers.

† Varieties in which the heterogeneous or "X" type of infection occurred were counted as half resistant.

This relation is shown also by correlations between the number of varieties resistant to physiologic forms and the percentages of apical swellings produced by them. Including all forms shown in Table IV and Figure 11, $r = + .265 \pm .144$.

The discrepancies in these results are of special importance in that they occurred also in some other series to be discussed below. It is evident that forms 9, 27, and 39 constitute exceptions to the general results. Considering only the other forms in Figure 11, it would appear that form 27 produced fewer apical swellings than would be expected while forms 9 and 39 produced many more. These aberrant forms were tested repeatedly, and the results confirmed the values shown. Two different isolations of form 39 have been tested (Table IV), with almost identical results. The validity of the apparently aberrant figures appears unquestionable.

Considering again only the general course of the results, form 15 appears also to lie at a definite distance above the expected curve. It is to be noted further that Vernal emmer is resistant to almost all of the identified physiologic forms of *P. graminis tritici.* Of the first 43 forms studied by Stakman, Levine, and their associates, there are only 6 to which this variety is susceptible. The 4 forms included in these studies are indicated in Figure 11 by circles around the form numbers. Of these 4 forms, 3 were aberrant to the general course of the results. Whether this relation is other than fortuitous remains to be determined and will be discussed further below; but for the present we may assume that those forms that attack Vernal emmer successfully have some common characteristic which differentiates them from most of the other forms of *P. graminis tritici.* This common characteristic so affects the growth of these forms in plain agar drop cultures that the production of apical swellings is not indicative of the host ranges of the forms. If we omit from the calculation those forms to which Vernal emmer is susceptible, the correlation becomes much higher, $r = + .597 \pm .112$. If we further omit form 39, tho without explaining why it should be grouped with the "Vernal emmer group," the correlation becomes appreciably higher again, $r = + .791 \pm .067$.

These results indicate strongly that in *P. graminis tritici* the physiologic forms that are weaker pathogenically, if that term may be used in speaking of forms with relatively more restricted host ranges, produce high percentages of apical swellings on uredinial germ tubes in plain, one per cent agar; while forms with wide host ranges produce fewer of these apical, teliospore-like bodies. A definite group of physiologic forms, including form 39 and those tested to which Vernal emmer is susceptible, do not fit this general correlation. In view also of further results with these forms, it appears probable that they differ in some fundamental physiologic relation from the many others that have been studied. Whether this difference involves factors that are concerned also in parasitism, or is merely a peculiarity of response to cultural conditions that masks the usual correlation, cannot be stated from the results at hand.

Puccinia graminis tritici in Extracts from Host Plants

The concept of the physiologic nature of resistance to rusts has rested to a certain extent on negative evidence. Varietal resistance to the different physiologic forms of *P. graminis tritici* could not be explained in other ways, as for instance, by morphologic characteristics of the host; the hypothesis that resistance is owing at least in part to differences in the value of different plants as substrata for the rusts remained as a possible explanation. The significant differences were variously assumed to be materials present or produced in resistant plants, but absent in other plants, which inhibited growth of the parasite (33); or materials present only in susceptible plants, which furnished nutrients necessary to the development of the fungus (17).

Direct attack on the problem was attempted in the present work by culturing urediniospores of various physiologic forms of *P. graminis tritici* in extracts from different wheat varieties. Introductory series were run first, mostly with extracts expressed after freezing the tissues. The results appeared of some value, but were finally considered inconclusive as the methods used were in process of development and each successive refinement tended to throw doubt on the validity of earlier data. Thus, it was found that anastomosis of adjacent sporelings resulted in longer growth than that secured from a single spore, so that for length of germ tube measurements it was necessary to select spores well separated in the drop cultures. The discovery that the length of germ tubes is influenced by the density of inoculum, made it desirable to count the number of spores in each drop, for accurate comparison.

The preliminary series were, however, of some value in addition to that of affording the opportunity of perfecting the technique. They showed that germination counts were much more variable, within presumably similar conditions, than growth measurements. In view also of the fact that germination of rust spores occurs readily in distilled water, and apparently with little regard to host relations, germination counts were not included in the later experiments.

It was found that wheat extracts required considerable dilution before urediniospores could germinate and growth occur (illustrated also in Tables VI, VIII-XII, XVI, and XVII). Growth was often poorer in extracts diluted to .05 than in the checks; while in further dilutions to .005 it was considerably better than in check cultures. Minute proportions of host-plant extracts were thus sufficient to influence the growth of the rust.

The following experiments were performed with the improved methods described and have furnished direct evidence that there is a physiologic basis for resistance to Uredinales.

Experiment I

Methods: Kanred and Mindum wheat were sown in rows in the field, August 17, 1926. The plants were exposed to natural infection, but were attacked to a very slight extent, if at all, before harvest. The dates of harvest and methods of extraction used for the different lots are given in Table V. It is to be noted that the extracts in lots 2, 6, 7, and 8 were not diluted during preparation, while the decoctions of lots 3, 4, 5, and 9 were necessarily in water; and that these differences in original concentration of the plant extracts were disregarded in the further dilution for culture substrata. All materials were used as prepared, and in further dilutions with sterile, distilled water to .25, 0.1, .01, and .001, as substrata for hanging-drop cultures of physiologic forms 18 and 19 of *P. graminis tritici*. Duplicate hanging-drop cultures were inoculated with urediniospores of each physiologic form with each dilution of each extract or decoction. The two wheat varieties react reciprocally to these physiologic forms. Kanred is susceptible to form 18 and practically immune from form 19, while Mindum is resistant to form 18 and susceptible to form 19.

TABLE V

PROCEDURES USED IN EXPERIMENT I FOR THE PREPARATION OF EXTRACTS FROM KANRED AND MINDUM SEEDLINGS

Lot	Material	Preparation	Sterilization
2*	Mindum plants, cut September 25	Ground; pressed in Monel metal cups by direct hand pressure only	Filtered aseptically through sterile filter paper
3	200 gm. plants, cut September 28	Ground; steamed in 500 cc. distilled water in Arnold sterilizer, 2 hours; filtered through cheesecloth and filter paper	Autoclaved 15 minutes at 15 pounds pressure
4	200 gm. plants, cut September 29	Ground; steeped in 500 cc. cold, distilled water, at 22° C., 4½ hours; strained through cheesecloth	Ultrafiltered through Berkefeld filter
5	200 gm. plants cut September 29	Ground; steeped in 500 cc. cold, distilled water, at 22° C., 4½ hours; strained through double cheese-cloth and double filter paper	Autoclaved 15 minutes at 15 pounds pressure
6	500 gm. plants, cut October 10	Ground; pressed at 0 pressure (hand pressure only); filtered through filter paper	Ultrafiltered through Berkefeld filter
7	(Material left in press from lot 6)	Pressed at 0-50 kgm. per cm.^{2} in hydraulic press; filtered through filter paper	Ultrafiltered through Berkefeld filter
8	(Material left in press from lot 7)	Pressed at 50-150 kgm. per cm.^{2} in hydraulic press; filtered through filter paper	Ultrafiltered through Berkefeld filter
9	(Material left in press from lot 8)	Stored two days in refrigerator; heated in 500 cc. distilled water in autoclave, 15 minutes at 15 pounds; decanted; filtered hot through filter paper	Autoclaved 15 minutes at 15 pounds pressure

* Mindum only in this lot; all others apply to Kanred and Mindum.

Length of germ tube results.—The length of germ tube measurements of these series have been studied in some detail (Tables VI to XIII). As shown above, germ tubes of form 18 sporelings are longer than those of form 19 when grown in purely synthetic media and under precisely similar conditions. Direct comparison of the growth in plant extracts would therefore be misleading and difficult to interpret. We might obviate this difficulty by comparing the magnitudes of differences observed here between the two forms with those observed between the checks—cultures in distilled water—in each series. However, it was also shown above that the lengths of germ tubes in drops of sterile, distilled water, as of other media, are greatly affected by the numbers of urediniospores used in inoculating the drops. The following proved an expeditious way of correcting simultaneously for both of these factors.

TABLE VI

NET INCREASES IN LENGTHS OF GERM TUBES OF *P. graminis tritici* FORMS 18 AND 19 IN EXTRACTS FROM KANRED AND MINDUM WHEAT, DILUTED IN STERILE, DISTILLED WATER*

Lot No.	Wheat extracts	Physiologic forms of *P. graminis tritici*	Net increases in lengths of germ tubes, in microns, in extracts diluted to concentrations indicated					
			Mean, all concentrations	1.0	.25	.1	.01	.001
2	Mindum	18	48	....	....	162	—30	12
		19	299	....	363	498	196	138
3	Kanred	18	36	....	—58	46	48	106
		19	132	....	....	107	162	128
	Mindum	18	41	—70	—49	218	94	10
		19	38	....	112	—53	160	—68
4	Kanred	18	230	....	63	442	394	22
		19	189	....	171	345	95	147
	Mindum	18	3	—10	60	24	—61	....
		19	96	....	164	177	73	—31
5	Kanred	18	86	—99	280	97	114	39
		19	1	—58	—101	68	114	—17
	Mindum	18	70	31	266	—5	10	49
		19	31	—90	157	15	102	—31
6	Kanred	18	287	....	191	176	324	457
		19	147	....	142	162	193	92
	Mindum	18	0	....	....	—80	82	—2
		19	53	....	....	—191	12	339
7	Kanred	18	154	....	38	162	70	346
		19	105	....	72	242	76	29
	Mindum	18	39	....	53	—38	17	123
		19	82	....	....	—43	193	97
8	Kanred	18	—59	....	....	....	—20	—99
		19	—56	....	....	—92	19	—94
	Mindum	18	175	....	235	....	287	2
		19	89	....	....	31	143	94
9	Kanred	18	—79	—234	51	2	—147	—65
		19	0.5	....	41	46	—128	43
	Mindum	18	—112	—141	—107	—104	—15	—191
		19	3	....	—9	—27	25	22

* Recorded lengths, minus (distilled water) checks estimated for the actual densities of inoculum of the individual cultures, minus the mean divergence of actual checks of particular series from estimated values for these checks.

TABLE VII

Net Increases in Lengths of Germ Tubes on Kanred and Mindum Substrata, as Compared to Estimated Growth in Sterile, Distilled Water, Expressed as Mean Values, Including All Cultures in the Series and Disregarding the Varying Dilutions of Substrata

Wheat extracts	Physiologic forms of *P. graminis tritici*	Means of increases in lengths of germ tubes, in microns					
		All lots		Lots 2, 4, 6, 7, and 8 (not heated during preparation)		Lots 3, 5, and 9 (heated during preparation)	
		(a)*	(b)*	(a)	(b)	(a)	(b)
Kanred	18	121	98	197	183	9	13
	19	86	72	86	107	74	31
Mindum	18	8	26	45	49	—46	—0.3
	19	39	86	86	133	—32	24

* (a) Increases estimated from checks calculated by formula only, that is, corrected for variations in density of inoculum but not for differences between series.

(b) Corrected also by divergence of the actual checks of the individual series from estimate (as in Table VI) so that results are completely comparable.

Tables of estimated length of germ tube values for different numbers of spores per drop of distilled water were calculated from the data of Figures 2 and 3 for the two forms. From these tables "estimated check values," which represented growth in distilled water drops containing the same numbers of spores as each hanging-drop culture under consideration, were selected for each of the duplicate cultures of each form. These estimated tube lengths were subtracted from the mean lengths of germ tubes in the cultures. This single subtraction corrected the measurements (1) for differences in the density of inoculum of different cultures, and (2) for the average difference between lengths of germ tubes of the two physiologic forms considered. After this subtraction, the results in duplicate cultures were averaged and thereafter considered together.

Up to this point the actual checks of the series were disregarded, largely to facilitate use of the correction for differences in density of inoculum. The checks could not be disregarded altogether since it was desired to put series run at different times on directly comparable bases, and the checks of individual series usually showed a tendency for series as a whole to diverge in one direction or the other from the averages used in calculating the estimated checks. Comparing the actual check measurements of series with estimated checks of the same densities of inoculum, definite figures were therefore obtained which represented the divergence of each check from the average. Averaging the individual divergences, a figure was secured which represented the mean divergence of the series for each form; and this was used to correct the results in the wheat extracts throughout the series. The "net increases in length of germ tubes" obtained after this second correction, listed in Table VI, appear as nearly perfectly comparable as possible with the information at hand. In the specific case of the two form-18 drop cultures in lot 6, Kanred extract, diluted to .01 in distilled water, the calculations involved were as given below:

	Culture a	Culture b	
Means of original measurements of lengths of germ tubes (there was unusually close agreement of duplicates here.)	518μ	513μ	
Number of urediniospores per drop	69	50	
Estimated check values, that is, estimated lengths of germ tubes in distilled water drops of corresponding densities of inoculum	181μ	165μ	
Recorded lengths minus estimated checks	337μ	348μ	
Average for the duplicate cultures			343μ
Divergences of measurements in actual check cultures of this series from estimated checks with the same density of inoculum as the actual checks			− 53μ + 92
Sum of divergences			+ 39
Mean divergence, for the series			+ 19μ

$343\mu - 19\mu \doteq 324\mu$, the net, corrected increase in length of germ tubes as used in Table VI.

The final corrected values indicate the increases only and are therefore smaller than the actual recorded lengths. Positive values indicate longer growth than in the checks and negative values the reverse.

It is evident from Table VI that the effect of extracts of either variety was usually to increase the length of germ tubes of both forms except in the most concentrated of the extracts of each series in which growth occurred. In Kanred extracts the increase was usually greater with form 18 than with form 19, but in Mindum extracts the greater increase was usually with form 19. This is demonstrated by the mean values for the different series, and for the experiment as a whole in Table VII, in which all the net increases from Table VI are averaged. Table VII includes also averages of results calculated without correction for the divergence of the actual checks from estimated check values. By both methods there was an average greater growth of form 18 in the Kanred series and of form 19 in the Mindum series. By both methods of calculation, this was true of the combined increases in lots 2, 4, 6, 7, and 8, which were not heated during preparation. With lots 3, 5, and 9, on the other hand, the increases in the case of form 19 were greater than those of form 18 in the Kanred series as well as in the Mindum series.

The results given in Table VI were also considered by comparing the increase in each solution for the two forms. This was conveniently done by subtracting each form-19 "net increase" from the corresponding form-18 value. Positive differences indicate that in the particular substratum there were greater increases with germ tubes of form 18 than with those of form 19; negative differences indicate the reverse (Table VIII). Therefore, both the positive values shown for most of the Kanred extracts and the negative values for most of the Mindum extracts agree with the hypothesis that length of germ tubes is increased to a greater extent in extracts from susceptible plants than in those from resistant plants.

TABLE VIII

DIFFERENCES BETWEEN NET INCREASES IN LENGTHS OF GERM TUBES OF FORMS 18 AND 19*

Lot No.	Wheat extracts	Differences between increases for forms 18 and 19, in microns, in extracts diluted to concentrations indicated					
		Mean, all concentrations	1.0	.25	.1	.01	.001
2	Mindum	—278	....	....	—336	—226	—126
3	Kanred	—66	....	....	—61	—114	—22
	Mindum	31	....	—161	271	—66	78
4	Kanred	41	....	—108	97	299	—125
	Mindum	—130	....	—104	—153	—134	....
5	Kanred	85	—41	381	29	0	56
	Mindum	6	121	109	—20	—92	80
6	Kanred	140	....	49	14	131	365
	Mindum	—53	....	....	111	70	—341
7	Kanred	49	....	—34	—80	—6	317
	Mindum	—48	....	....	5	—176	26
8	Kanred	—22	....	....	....	—39	—5
	Mindum	26	....	....	....	144	—92
9	Kanred	—40	....	10	—44	—19	—108
	Mindum	—107	....	—98	—77	—40	—213

* Net increases, as given in Table VI, for form 19 were subtracted from the corresponding values for form 18.

Further condensation of results was obtained by subtracting the Mindum values from the corresponding Kanred values of Table VIII. These final subtractions yielded single figures, as given in Table IX, for each dilution of each lot, representing the summation of the differentiation between form 18 and form 19 in both the Kanred and the Mindum extracts prepared by the various methods. The series of subtractions involved in this summation of differentiation is expressed in the following algebraic equation, in which all the original values are of the net increases in lengths of germ tubes, as given in Table VI:

$$\text{summation} = (\text{form } 18_{\text{Kanred}} - \text{form } 19_{\text{Kanred}}) - (\text{form } 18_{\text{Mindum}} - \text{form } 19_{\text{Mindum}}).$$

Positive values obtained by this method indicate that elongation was increased to a greater extent in the extracts from susceptible varieties, and negative values that it was increased to a greater extent in extracts from the resistant varieties. In Table IX positive numbers predominate. The largest numbers, indicating most decided preferential elongation in susceptible rather than resistant extracts, are in the lots in which extracts were prepared without heating, that is, lots 4, 6, 7, and 8.

TABLE IX

SUMMATION OF LENGTH OF GERM-TUBE RESULTS OF EXPERIMENT 1, WITH VALUES CORRECTED, AS FOR TABLES VI AND VIII, FOR VARIATIONS IN DENSITY OF INOCULUM AND ALSO FOR DIVERGENCES OF SERIES FROM ESTIMATED MEANS*

Lot No.	Summation of length of germ tube results, in microns, in extracts diluted to concentrations indicated					
	Mean, all concentrations	1.0	.25	.1	.01	.001
3	−160	....	....	(−332)	−48	−100
4	226	....	(−4)	250	433	....
5	45	(−162)	272	49	92	−24
6	223	....	....	(−97)	61	706
7	125	....	....	(−85)	170	291
8	−48	....	....	....	(−183)	87
9	67	....	(108)	33	21	105

* Differences between net increases in lengths of germ tubes of forms 18 and 19, as given in Table VIII, for Mindum substrata were subtracted from the corresponding values for Kanred substrata. Positive numbers resulting from this final subtraction indicate that elongation was increased to a greater extent in extracts from susceptible varieties, negative numbers that it was increased to a greater extent in extracts from resistant varieties.

More decisive, and perhaps more accurate, comparison of lots is obtained when the last figures to the left in each row of the results in the individual dilutions (the figures in parentheses in Tables IX-XII) are omitted. It will be noted that the values are quite generally at variance with the others of the series. This is owing perhaps in part to the direct effect of the more concentrated extracts in inhibiting growth to such an extent as to obscure differences due to the varietal sources of the extracts, and in part to the fact that these numbers were of necessity based on fewer measurements than in the case of growth in more dilute substrata, since germination as well as growth was reduced in the higher concentrations. Considering, then, only those numbers to the right of the numbers in parentheses, it is to be noted that all the negative ones are included in the series in which the extracts were heated.

Tables X, XI, and XII were calculated to show that the results above were not based on errors due to the method of calculation. These tables are final summations of the results of subtractions as used in

TABLE X

Length of Germ Tube Results of Experiment 1. Summation as in Table IX, Except with Values Corrected for Individual Variations in Density of Inoculum by the Use of Estimated Checks, But Not Corrected for Series Divergences

Lot No.	Summation of length of germ tube results, in microns, in extracts diluted to concentrations indicated					
	Mean, all concentrations	1.0	.25	.1	.01	.001
3	—62	....	....	(—234)	51	—2
4	227	....	(—3)	251	433	....
5	—48	(—254)	179	—43	—2	—119
6	171	....	....	(—99)	19	592
7	227	....	....	(46)	278	358
8	137	....	....	....	(7)	268
9	—41	....	(63)	—97	—106	—24

TABLE XI

Length of Germ Tube Results of Experiment 1. Summation as in Table IX, Except with Values Corrected by the Actual Check Cultures of Each Series and Not Corrected for Variation in Density of Inoculum

Lot No.	Summation of length of germ tube results, in microns, in extracts diluted to concentrations indicated					
	Mean, all concentrations	1.0	.25	.1	.01	.001
3	—14	....	....	(—235)	116	78
4	227	....	(22)	222	438	....
5	—5	(—70)	205	—26	—53	—80
6	176	....	....	(—17)	—17	562
7	30	....	....	(—97)	32	155
8	—80	....	....	....	(—228)	68
9	143	....	(307)	92	70	104

TABLE XII

Length of Germ Tube Results of Experiment 1. Summation as in Table IX, Except with Original, Uncorrected Values*

Lot No.	Summation of length of germ tube results, in microns, in extracts diluted to concentrations indicated					
	Mean, all concentrations	1.0	.25	.1	.01	.001
3	—82	....	....	(—304)	48	10
4	233	....	(22)	222	455	....
5	47	(—26)	266	20	9	—36
6	262	....	....	(109)	118	558
7	152	....	....	(24)	153	278
8	203	....	....	....	(46)	360
9	2	....	(150)	—61	—32	—49

* The values tabulated here from the uncorrected measurements are the same as would be obtained by still another method of calculation, the use of an averaged check value for all form 18 cultures and a similar mean check for all form 19 cultures, as such average check corrections cancel out in the repeated subtraction used in the summation.

preparing Table IX, but differ in that the original values used in these subtractions were calculated again, independently, by the various methods indicated. Thus, Table X is based on the original measurements corrected only for variations in density of inoculum and for the average difference between forms 18 and 19, without using the actual checks of the series at all, thus obviating the possibility of bias from them; Table XI is based on measurements corrected only with the actual checks of the series; and Table XII is based on original, uncorrected values.

Surprisingly close agreement was obtained by these various methods of calculating the results. Throughout the four tables, only one negative value was obtained for any of the concentrations to the right of the parentheses in lots 4, 6, 7, and 8. In the lots that were heated during preparation. on the contrary, there were 17 negative values. Averages of the results for the two series of extracts are given in Table XIII and demonstrate again the validity of the conclusion above. Irrespective of the method of calculation used, results in the unheated series are definitely in agreement with the hypothesis that elongation is increased to a greater extent in extracts from susceptible varieties. The lowest value obtained for the average increase was 104μ, and the highest, 314μ. It is to be remembered, however, that this is the sum of the average increase or decrease of both forms in both the Kanred and Mindum extracts.

TABLE XIII

Means of Tabulated Summations of the Effect of Kanred and Mindum Extracts in Differentiating Forms 18 and 19 by the Increases in Lengths of Germ Tubes[*]

Corrections applied to individual values	Means of summations, in microns			
	Lots 4, 6, 7, and 8 (unheated in preparation)		Lots 3, 5, and 9 (heated in preparation)	
	(a)[†]	(b)[†]	(a)	(b)
For variations in density of inoculum and by actual check values (Table IX)	148	285	1	44
For variations in density of inoculum only (Table X)	195	314	−49	−18
By actual check values only (Table XI)	104	209	42	56
Uncorrected (Table XII)	213	306	−0.5	19

[*] Positive numbers indicate that elongation was increased to a greater extent in extracts from susceptible varieties, negative numbers that it was increased to a greater extent in extracts from resistant varieties.

[†] (a) Including all cultures of the series.

(b) Excluding results in the highest concentration of the substrata in each series in which comparison was possible.

With the series that were heated during preparation no such consistent differentiation was secured. The results for the different lots varied with the methods of calculation, and the averages in Table XIII show that in these series there was only negligible, if any, tendency for increase in elongation to be associated with the resistance or susceptibility of the varieties to the physiologic forms.

Branching ratios.—Germ tubes of form 19 characteristically branch more than those of form 18 on most substrata. This was true in the present experiment, both in dilutions of the plant extracts and in sterile distilled water. Branching ratios—total lengths of branches divided by lengths of main germ tubes—for corresponding cultures in the same medium were often 10 to 20 times larger for form 19 than for form 18, with occasional ratios as large as .23 and .36 for form 19 in solutions in which the promycelia of form 18 did not branch at all. Table XIV lists these results as net increases or decreases, obtained by subtracting the ratios for the check cultures of the individual series from the respective ratios in extracts. The values here are therefore directly comparable between forms and presumably between series.

TABLE XIV

NET INCREASES IN BRANCHING RATIOS, *P. graminis tritici* FORMS 18 AND 19, IN EXTRACTS FROM KANRED AND MINDUM WHEAT, DILUTED IN STERILE, DISTILLED WATER*

Lot No.	Wheat extracts	Physiologic forms of *P. graminis tritici*	Net increases in branching ratios, in extracts diluted to concentrations indicated					
			Mean, all concentrations	1.0	.25	.1	.01	.001
2	Mindum	18	.087	.....	.....	0	.16	.10
		19	.172	.....	—.10	—.07	.23	.63
3	Kanred	18	.085	.....	.31	.14	—.06	—.05
		19	.287	.....	.....	.29	.22	.35
	Mindum	18	—.044	—.12	.07	—.06	0	—.11
		19	—.180	.....	—.04	—.27	—.14	—.27
4	Kanred	18	.007	.....	—.01	.01	—.01	.04
		19	.065	.....	0	—.09	.20	.15
	Mindum	18	.017	—.02	—.02	.07	.04	.....
		19	.030	.....	.01	.11	—.04	.04
5	Kanred	18	.042	—.05	—.01	.07	0	.20
		19	.120	—.03	.25	.07	.15	.16
	Mindum	18	.009	—.10	—.055	.31	—.10	—.01
		19	—.021	—.17	—.085	—.07	.02	.20
6	Kanred	18	—.041	.....	—.065	—.045	—.02	—.035
		19	—.036	.....	—.115	—.005	—.03	.005
	Mindum	18	.011	.....	.....	.057	—.003	—.02
		19	.015	.....	.....	—.13	.13	.045
7	Kanred	18	—.065	.....	—.05	—.08	—.05	—.08
		19	.039	.....	—.045	.035	.045	.12
	Mindum	18	.027	.....	.04	0	.06	.01
		19	.070	.....	.....	.20	—.01	.02
8	Kanred	18	0	.....	.....	.....	—.01	.01
		19	.017	.....	.....	.01	—.02	.06
	Mindum	18	0	.....	—.02	.....	—.01	.03
		19	—.057	.....	.....	—.02	—.10	—.05
9	Kanred	18	.060	—.05	—.01	.35	.05	—.04
		19	.290	.....	.26	.31	.60	—.01
	Mindum	18	.082	—.01	—.07	.32	.12	.05
		19	.225	.....	—.18	.97	.06	.05

* Branching ratios = total lengths of branches divided by lengths of main germ tubes. Increases figured from branching ratios in distilled water checks of the individual series.

As there is only very slight correlation of branching ratios with the number of spores per drop, corrections for variations in density of inoculum were unnecessary.

In all the 7 Kanred series, the means of increases in branching ratios for form 18 were lower than for form 19. In 4 of the corresponding Mindum series, also, the increases for form 18 were smaller than those for form 19, but in each of these cases the difference was less than in the respective Kanred series. There is a tendency for branching ratios to be greater in extracts from the resistant varieties than in extracts from susceptible varieties.

This relation is more readily evident in Table XV, in which are listed the differences between corresponding branching-ratio increases for forms 18 and 19. Positive values indicate that branching of form 18 increased more than that of form 19, negative values the reverse. In the Kanred series there are accordingly 18 negative values and only 7 positive values, while in the Mindum series there are 17 positive to the 10 negative values. Moreover, comparing the Kanred with the Mindum values, it will be noted that the latter are almost always larger. This is true with the means for the series in all except lot 6, where the difference is negligible.

TABLE XV

DIFFERENCES BETWEEN NET INCREASES IN BRANCHING RATIOS OF FORMS 18 AND 19*

Lot No.	Wheat extracts	Differences between increases in branching ratios, for forms 18 and 19, in extracts diluted to concentrations indicated						Average differentiation: Kanred mean minus Mindum mean
		Mean, all concentrations	1.0	.25	.1	.01	.001	
2	Mindum	—.210	.....	.....	.07	—.17	—.53	.....
3	Kanred	—.277	.....	.....	—.15	—.28	—.40	—.432†
	Mindum	.155	.....	.11	.21	.14	.16	
4	Kanred	—.057	.....	—.01	.10	—.21	—.11	—.060‡
	Mindum	.003	.....	—.03	—.04	.08	.....	
5	Kanred	—.078	—.02	—.26	0	—.15	.04	—.108†
	Mindum	.030	.07	.03	.38	—.12	—.21	
6	Kanred	—.002	.....	.050	—.040	.01	—.03	.002‡
	Mindum	—.004	.....	.....	.187	—.133	—.065	
7	Kanred	—.092	.....	.040	—.115	—.095	—.20	—.045‡
	Mindum	—.047	.....	.....	—.20	.07	—.01	
8	Kanred	—.020	.....	.....	.....	.01	—.05	—.105‡
	Mindum	.085	.....	.....	.....	.09	.08	
9	Kanred	—.205	.....	—.27	.04	—.55	—.04	—.360†
	Mindum	.155	.....	.11	.21	.14	.16	

* Net increases, as in Table XIV, for form 19 subtracted from corresponding values for form 18.

† Extracts heated during preparation.

‡ Extracts not heated during preparation.

Comparison of results with regard to the heating of extracts during preparation is of interest. When the means of values for the Mindum cultures are subtracted from those for the Kanred cultures, values are obtained which represent the average of all differentiation for each lot, as indicated in the last column of Table XV. There was better differentiation of forms to which the varieties are susceptible or resistant in the extracts that had been heated during preparation (lots 3, 5, and 9) than in the others (lots 4, 6, 7, and 8)—an effect exactly opposite to that noted in the differentiation on the criterion of increase in length of germ tubes.

Summary of Experiment 1.—In hanging-drop cultures with extracts from normal Kanred wheat plants, germ tubes of form 18 were increased in length, as compared with check cultures, to a greater extent than was the case with germ tubes of form 19 as compared to checks of form 19. In Mindum extracts, elongation of form 19 was correspondingly favored more than that of form 18. The average length of germ tubes increased more, in each case, in the extract from the susceptible variety. This relation appeared in the original measurements and still held when results were corrected for differences in density of inoculum, for differences between series, etc. The branching ratios, on the other hand, were increased to a greater extent in extracts from resistant varieties.

Experiment 2

Another series of plant extracts was prepared from Kanred, Mindum, and Little Club wheat seedlings, planted in the greenhouse May 21 and cut June 6, 1927. Approximately the same method of extraction was used as that for lot 4 of Experiment 1 (Table V). Plants were cut, washed with distilled water, ground, steeped for 3 hours in a quantity of distilled water equal to 2½ times the green weight of the plants, the liquid squeezed by hand through cheesecloth and ultrafiltered. Since some of the distilled water used in washing the plants always remained, the final filtrates were assumed to contain about .25 concentration of actual plant extract, and further dilution was made on this basis. Each extract was diluted in plain one per cent agar to final concentrations of .1, .01, and .001 for drop cultures. Three physiologic forms of *P. graminis tritici* were used as inoculum. The actual reactions of plants of the three varieties to these forms is shown in the following scale, running from "0" for immunity to "4" for extreme susceptibility:

Physiologic form	Little Club	Kanred	Mindum
1	4	0	1
18	4	4=	1=
19	4	0;	4=

The lengths of germ tubes produced in drop cultures of the extracts are given in Table XVI. These measurements have been corrected for variations in density of inoculum (using the averaged regression value derived from study of a number of forms of *P. graminis tritici* on agar drops, as explained above, Table II). They are thus directly comparable, each representing the residual length of germ tubes after all increase from density of inoculum has been removed; or in other words, representing the residual "constant" at the base, or at "0" number of spores per drop, of a number-of-spores to mean-length-of-germ-tube graph for each form on each substratum.

TABLE XVI

Lengths of Germ Tubes of Physiologic Forms 1, 18, and 19 of *Puccinia graminis tritici* in Extracts from Three Wheat Varieties, Diluted in Plain One Per Cent Agar*

Wheat extracts	Physiologic forms of *P. graminis tritici*	Lengths of germ tubes, in microns: In extracts diluted to concentrations indicated: .1	.01	.001	In plain agar checks
Little Club	1	264	165	211	249
	18	351	405	457	247
	19	245	373	235	332
Kanred	1	99	127	125	134
	18	344	198	179	331
	19	152	230	209	255
Mindum	1	234	445	400	408
	18	323	460	512	606
	19	211	406	427	358

* Corrected for variations in density of inoculum.

The values given in Table XVII have been further corrected for differences between the series by subtracting from each measurement for a diluted extract the check value for the particular series.

TABLE XVII

Increases in Lengths of Germ Tubes of Physiologic Forms 1, 18, and 19 in Extracts from Three Wheat Varieties Diluted in One Per Cent Agar, as Compared to Lengths in Checks*

Wheat extracts	Physiologic forms of *P. graminis tritici*	Increases in lengths of germ tubes, in microns, in extracts diluted to concentrations indicated: Mean, all concentrations	.1	.01	.001
Little Club	1	−36	15	−84	−38
	18	157	104	158	210
	19	−48	−87	41	−97
Kanred	1	−17	−35	−7	−9
	18	−91	13	−133	−152
	19	−58	−103	−25	−46
Mindum	1	−48	−174	37	−8
	18	−174	−283	−146	−94
	19	−10	−147	48	69

* Corrected values, from Table XVI, for mean lengths of germ tubes in extracts, minus the respective lengths in check cultures.

In this experiment, the extracts generally inhibited growth as compared to that in the checks. Of the 27 sets of cultures in extracts, growth was less than that of the checks in 18, as shown by minus numbers in Table XVII. There was increased growth in only 9 cases. Of these, 8 were in the 15 sets with forms in extracts from varieties susceptible to those forms; while only one case, form 1 in .01 concentration of Mindum extract, was in the 12 sets of cultures in extracts from resistant plants. The average of growth minus that of respective checks for all cultures in susceptible extracts was about — 5μ, or, even omitting the form 18 series in Little Club extracts, in which there were exceptional increases, only — 46μ; while for cultures in resistant extracts the average was — 74μ. It may be mentioned that this relation appeared also when the original data were tabulated without correction for differences in density of inoculum. The average in this case for all cultures in susceptible extracts was — 27μ, and for cultures in resistant extracts, — 67μ.

The relative branching of germ tubes in this experiment was studied in considerable detail; but these results appeared of little significance. The greatest decreases in branching ratios in the extracts as compared to those in the checks occurred in extracts from varieties susceptible to the respective forms, but so also did the greatest increases. The average of increases for all forms in all dilutions of varieties susceptible to them was .009, and for all forms in extracts from resistant plants, .012. This difference, tho slight, was in agreement with the results of Experiment 1.

Differentiation between forms to which varieties are resistant or susceptible was definite in this experiment only by the criterion of length of germ tubes. As in Experiment 1, the germ tubes were longer in extracts from susceptible varieties than in those from resistant varieties.

Experiment 3

The Mindum extract from Experiment 2 was used here with a larger number of physiologic forms. Lengths of germ tubes for 10 forms of *P. graminis tritici* are given in Table XVIII. In the 10 per cent concentration used, the Mindum extract decreased the growth of most of the forms to a point below that of the respective checks in plain agar.

The forms tested, however, grouped definitely into two series, with the differences in length running from + 58μ to — 93μ in one group and from — 165μ to — 203μ in the other. Of the seven forms to which Mindum is susceptible, there were five in the group of forms whose germ tubes were only slightly decreased in size; while of the three forms to which Mindum is resistant, there were two with the

TABLE XVIII

LENGTHS OF GERM TUBES, CORRECTED FOR VARIATIONS IN DENSITY OF INOCULUM, OF SOME PHYSIOLOGIC FORMS OF *P. graminis tritici* IN PLAIN-AGAR DROPS AND IN AGAR CONTAINING 10 PER CENT OF AN EXTRACT FROM MINDUM WHEAT

Physiologic forms of *P. graminis tritici*	Lengths of germ tubes, in microns		Increase or decrease in lengths of germ tubes, in microns, (length in Mindum agar minus that in checks) of forms to which Mindum is	
	10 per cent Mindum agar	Plain-agar checks	Susceptible	Resistant
1	131	319	....	−188
9	136	225	−89	....
15	211	414	−203	....
17	171	251	−80	....
18	197	362	....	−165
19	230	301	−71	....
21	183	276	−93	....
27	152	94	....	+58
34	61	118	−57	....
39	79	251	−172	....

more considerable decreases. The results then confirm in general the validity of the assumption that changes in cultural characteristics of forms in extracts from different varieties are to be attributed to the resistance relations of the varieties to the forms rather than to accidental variation.

The three discrepancies in Table XVIII are of particular interest. In correlation of the host ranges of a number of physiologic forms with the production of apical swellings by the same forms in drop cultures in plain agar (Fig. 11), all except four physiologic forms gave a comparatively close fit to a linear correlation. The four exceptions included three of the four forms studied to which Vernal emmer is susceptible (forms 9, 15, and 27) and form 39. In the present series, the three discrepancies include two of three forms studied to which Vernal emmer is susceptible (forms 15 and 27) and form 39.

Branching ratios for the series are listed in Table XIX. As before, there was general differentiation between the forms to which Mindum is susceptible and those to which it is resistant. The branching ratios were lowered with most of the forms in the first group, and raised with two of the three forms in the second group. There were three definite discrepancies. These again included form 39 and two of the forms to which Vernal emmer is susceptible, this time forms 9 and 27.

Differentiation by the percentages of teliospore-like bodies produced (Table XX) was not so uniform as with the other two criteria. It is probable that with most forms the production of apical bodies is increased to a greater extent in extracts from resistant varieties than in extracts from susceptible varieties. In the present series, coincident with the use of a substratum containing a high enough concentration of Mindum extract to decrease the length of germ tubes even of forms

TABLE XIX

Ratios, Total Lengths of Branches Over Lengths of Main Germ Tubes, of Some Physiologic Forms of *P. graminis tritici* in Plain Agar Drops and in Agar Containing Ten Per Cent of an Extract from Mindum Wheat

Physiologic forms of *P. graminis tritici*	Branching ratios		Increase or decrease (ratios in Mindum agar minus those of checks) of forms to which Mindum is	
	10 per cent Mindum agar	Plain-agar checks	Susceptible	Resistant
1	.005	.004	.....	+.001
9	.084	.013	+.071	.....
15	.023	.071	−.048	.....
17	.061	.080	−.019	.....
18	.008	.005	.....	+.003
19	.048	.089	−.041	.....
21	.025	.037	−.012	.....
27	.012	.035	.....	−.023
34	.062	.078	−.016	.....
39	.065	0	+.065	.....

to which Mindum is susceptible, there was increased production of apical bodies with most of the forms as compared to that in the checks. The greatest increase was with form 1, to which Mindum is resistant, and the apical bodies here also resembled teliospores unusually closely. The only definite decreases were with forms 21 and 39, to which Mindum is susceptible. The greatest discrepancies in the results were found again in the case of physiologic forms to which Vernal emmer is susceptible, forms 15 and 27.

TABLE XX

Percentage of Germ Tube Tips on Which the Teliospore-Like Apical Swellings Were Produced With Physiologic Forms of *P. graminis tritici* in Plain Agar Drops and in Agar Containing Ten Per Cent of Mindum Extract

Physiologic forms of *P. graminis tritici*	Production of apical bodies, in per cent		Percentage in Mindum agar minus that in checks; for forms to which Mindum is			
	10 per cent Mindum agar	Plain-agar checks	Susceptible		Resistant	
			Uncorrected	Corrected*	Uncorrected	Corrected*
1	72	18	....	....	+54	+49
9	85	70	+15	+22	....	....
15	57	17	+40	+36	....	....
17	45	25	+20	+19	....	....
18	15	0	....	....	+15	+5
19	5	0	+5	+18	....	....
21	15	27	−12	−17	....	....
27	19	8	....	....	+11	−6
34	24	5	+19	+12	....	....
39	7	43	−36	−12	....	....

* Counts for individual cultures corrected for density of inoculum to 50 spores per drop.

Considering this experiment as a whole, two outstanding relations appear. First, most of the forms, 6 of 10, were divided, as a result of comparison of the growth in drop cultures containing 10 per cent of Mindum extracts to that in plain agar checks, into groups which correspond definitely to the resistance of Mindum plants to the forms. Second, the greatest, and usually the only, discrepancies by all three criteria were in a definite group which included form 39 and those forms to which Vernal emmer is susceptible, and was identical with the group of forms found earlier to be aberrant to the usual correlation between rate of production of apical bodies and host-variety range.

Normal and Diseased Host Tissues as Sources of Extracts

Among theories on the nature of varietal resistance to rusts have been those postulating antibody action following infection. Two general hypotheses have been considered. First, antibodies produced under the stimulus of the parasite may inhibit the growth of rusts to which the plant is resistant. This inhibition may be supposed to act by direct attack on the parasite, in a manner more or less analogous to antibody resistance in animals; or by some indirect method such as increasing the sensitivity of adjacent host cells to the action of the parasite, with earlier death of these cells and eventual loss of nutrition for the pathogen. The second line of reasoning assumes that "antibody" formation, occurring perhaps only in the presence of physiologic forms of the rust to which the host is susceptible, produces in living host cells materials or conditions indispensable to the nutrition of the parasite. These materials might differ according to the plants and support the growth of only those rusts to which the hosts are susceptible. This second hypothesis would explain also the difficulty of growing rusts in artificial culture.

If either type of reaction actually is involved in resistance to rusts, extracts from plants attacked by rusts might include "antibodies"; and it is possible that such extracts might differentiate physiologic forms to which the host is resistant or susceptible more definitely than in the case of extracts from normal plants.

Material.—Kanred and Mindum wheat seedlings, grown in pots in the greenhouse during January to March, 1927, were used. Separate lots were used of the normal plants of each variety and of plants inoculated respectively with forms 18 and 19 of *P. graminis tritici* and grown in the greenhouse at the same time. Those inoculated with the different forms were separated from each other on the greenhouse bench only by glass partitions. Since it was desired that growth of the plants and also of the rusts with which the plants were inoculated should proceed under identical conditions for the three sets of each variety, and also that extracts should be tested as substrata for rusts within a few days of extraction, it was necessary to use seedlings of different ages for the different lots. Ages of the plants are given in Table XXI.

TABLE XXI

NORMAL AND DISEASED KANRED AND MINDUM WHEAT SEEDLINGS USED AS MATERIAL FOR EXTRACTS

Source of extract	Inoculated with *P. graminis tritici*	Age of plants when inoculated	Age of plants when cut	Infection record
		Days	Days	
Kanred	....	..	14	....
	Form 18	17	36	Abundant infection and sporulation
	Form 19	17	38	Hypersensitive flecking
Mindum	....	..	9	....
	Form 18	11	36	Hypersensitive flecking and necrosis
	Form 19	11	30	Abundant infection and sporulation

Method of extraction.—Plants were cut, weighed, placed in a clean funnel, and washed with a stream of distilled water to remove adherent spores and dust. They were then run through a meat grinder and mixed with an amount of distilled water three times the original green weight. The combined mass was pressed out between metal cups, using direct hand pressure only. The densely turbid, deep green fluid obtained was divided into two portions. The first was ultrafiltered through a Berkefeld filter, yielding a clear, straw-colored liquid. The second portion was passed through a single filter paper, using a previously heat-sterilized apparatus which prevented outside contamination. Usually the somewhat turbid, green filtrate still contained bacteria. The filtrates were stored in Pyrex tubes in the refrigerator and generally used within two days.

Cultures.—The filtrates themselves represented concentrations of approximately .25 that of the plant tissue; and further dilutions were made with sterile, distilled water to final concentrations of .1, .01, .001, and .0001. Hanging-drop cultures of forms 18 and 19 were made in duplicate with these dilutions of each filtrate.

Results.—Average estimated increases in lengths of germ tubes for each form on each substratum are given in Table XXII. As in previous series, germ tubes of form 18 increased in length to a greater extent in Kanred extracts than those of form 19, while in Mindum extracts, those of form 19 increased in length to the greater extent. In 26 sets of cultures of form 18 in the Kanred substrata, the germ tubes averaged 93 μ longer than those in estimated check cultures; while with form 19 the increases in the 25 pairs averaged only 32 μ. Again, in the Mindum extracts, the average with form 18 for 27 duplicated cultures was 12 μ, and 32 μ for 25 sets with form 19. These results agree with the susceptibility of Kanred to form 18 and its resistance to form 19, and the resistance of Mindum to form 18 and its susceptibility to form 19.

TABLE XXII

INCREASES IN LENGTHS OF GERM TUBES OF FORMS 18 AND 19 OF *P. graminis tritici* IN EXTRACTS, FROM NORMAL AND RUSTED WHEAT PLANTS, DILUTED IN STERILE, DISTILLED WATER*

Material	Filter	Physiologic forms of *P. graminis tritici*	Increases in lengths of germ tubes, in microns, in extracts diluted to concentrations indicated					
			Mean, all concentrations	.25	.1	.01	.001	.0001
Normal Kanred plants	Berkefeld	18	−76	....	−146	−121	....	39
		19	−102	....	−118	−169	....	−19
	Filter paper	18	−51	....	−130	−24	−61	12
		19	−77	....	−111	−164	−58	24
	Centrifuged, then Berkefeld	18	35	....	−49	−2	90	101
		19	17	....	−5	−2	−10	85
Kanred infected with form 18	Berkefeld	18	11	....	−46	124	36	−68
		19	31	−67	....	157	126	−90
	Filter paper	18	357	....	....	271	433	368
		19	171	....	−48	199	239	295
Kanred infected with form 19	Berkefeld	18	127	....	80	297	82	48
		19	−12	....	32	....	−26	−43
	Filter paper	18	272	....	246	287	329	225
		19	187	....	....	363	80	119
Normal Mindum plants	Berkefeld	18	−12	−138	−152	−44	133	140
		19	−30	....	−80	92	−60	−72
	Filter paper	18	−17	....	−176	−118	133	92
		19	10	....	−133	39	128	5
Mindum infected with form 18	Berkefeld	18	11	....	−38	−12	112	−17
		19	1	....	61	−70	−55	68
	Filter paper	18	−27	−14	−112	−53	0	46
		19	94	....	2	237	32	104
Mindum infected with form 19	Berkefeld	18	−25	−155	−102	98	56	−20
		19	4	−34	−3	−34	31	58
	Filter paper	18	163	....	220	293	206	−65
		19	114	....	−89	201	179	165

* Recorded lengths minus (distilled water) checks estimated for the same densities of inoculum.

Comparing the growth obtained in the different extracts given in Table XXII, it is to be noted that longer germ tubes were usually produced in the extracts filtered through filter paper than in corresponding extracts passed through the Berkefeld filter. Furthermore, differentiation between the length increases of forms 18 and 19 in the same extracts was almost always greater in the portions passed through filter paper only (Table XXIII). It is then perhaps permissible to consider the results in the paper-filtered series and to disregard the somewhat erratic results of the Berkefeld-filtered series.

It is evident as shown in Table XXII that longer germ tubes were produced in the extracts from the infected plants than in those from the normal plants. On the basis of these figures it would also appear that the longest growth occurs on extracts from plants inoculated with

TABLE XXIII

DIFFERENCES BETWEEN INCREASES IN LENGTHS OF GERM TUBES FOR FORMS 18 AND 19, *P. graminis tritici*, IN EXTRACTS FROM NORMAL AND RUSTED WHEAT PLANTS*

Material		Filter used	Differences between increases in length of germ tubes, in microns, in extracts diluted to concentrations indicated					
			Mean, all concentrations	.25	.1	.01	.001	.0001
Kanred plants	Normal	Berkefeld	26	....	—28	48	....	58
		Filter paper	27	....	—19	140	—3	—12
		Centrifuged, then Berkefeld	18	....	—44	0	100	16
	Infected with form 18	Berkefeld	—34	....	....	—33	—90	22
		Filter paper	113	....	....	72	194	73
	Infected with form 19	Berkefeld	50	....	—48	....	108	91
		Filter paper	93	....	....	—76	249	106
Mindum plants	Normal	Berkefeld	49	....	—72	—136	193	212
		Filter paper	—27	....	—43	—157	5	87
	Infected with form 18	Berkefeld	10	....	—99	58	167	—85
		Filter paper	—123	....	—114	—290	—32	—58
	Infected with form 19	Berkefeld	—28	—121	—99	132	25	—78
		Filter paper	49	....	309	92	27	—230

* Mean increases in lengths of germ tubes for form 18, corrected for variations in density of inoculum, minus similarly corrected means for form 19.

forms to which they are susceptible. Thus, in the Kanred series the average for form 18 in the extract from normal plants is — 51μ; in the extract from plants infected with form 19, 272μ; and in that from plants successfully attacked by form 18, 357μ. Similarly, both physiologic forms of *P. graminis tritici* produced longer germ tubes in the Mindum extracts from plants inoculated with form 19 than in the extracts from those inoculated but not infected with form 18, to which Mindum is resistant. Differences between the results obtained with extracts of plants inoculated with form 18 and those secured with extracts of plants inoculated with form 19 are not necessarily significant, since actual check cultures of these series were disregarded by the method of calculation of Table XXII; but the very large differences between growth in extracts of inoculated plants and growth in extracts of normal plants can hardly be considered accidental.

More accurate comparison of different series is possible with the differences between increases with form 18 and 19 than with the values themselves. In Table XXIII, the increases for form 19 in each substratum are subtracted from the corresponding values for form 18. Positive values indicate greater increases, or smaller decreases, for form 18, and negative values greater increases for form 19. As would be expected, the majority of such subtractions in the Kanred series gave positive values and the majority in the Mindum series negative values.

Averages for the differentiation in extracts prepared from the various materials by filtration through filter paper were as follows:

Kanred (form 18—form 19),	
Normal	27μ
Infected with form 18 (susceptible)	113
Infected with form 19 (resistant)	93
Mindum (form 18—form 19),	
Normal	—27
Infected with form 18 (resistant)	—123
Infected with form 19 (susceptible)	49

In both series, differentiation was definitely higher in the extracts from plants infected with form 18 than in the extracts from the normal plants. It may be noted that this relation, as well as the other results above, was still more definite when the results were calculated without using the corrections for variations in density of inoculum.

Branching-ratio results in the extracts from normal and diseased material are given in Table XXIV. As already noted, germ tubes of form 19 usually branch much more than those of form 18. This was evident again in the present experiment. In only one group of cultures of the 48 in which comparison is possible was there a higher branching ratio for form 18 than for form 19; while the form 19 ratio was higher in 42 cases.

It was also found above (Tables XIV and XV) that branching ratios were higher in the extracts from normal plants of resistant varieties than in extracts from susceptible varieties. In the present series, this was true except with the cultures of form 18 in extracts filtered through filter paper.

The branching ratios were influenced to a marked extent by the method of preparing the extracts. In every series, the averages for form 19 ratios (Table XXIV) were greater in the Berkefeld-filtered substrata than in those filtered merely through filter paper; while with form 18 the reverse was true in four of the six series. Differentiation of the two forms by the characteristic differences between the branching ratios was thus emphasized in the ultrafiltered extracts of most series.

Differences between branching ratios, with respect to the normal and diseased sources of substrata, were rather erratic. Branching-ratio values for differences between the two physiologic forms did not always vary inversely with the differences in lengths of germ tubes, as would have been expected from the other results. The relations

TABLE XXIV

BRANCHING RATIOS FOR FORMS 18 AND 19 OF *P. graminis tritici* IN EXTRACTS, FROM NORMAL AND RUSTED WHEAT PLANTS, DILUTED IN STERILE, DISTILLED WATER*

Material	Filter used	Physiologic forms of *P. graminis tritici*	Branching ratios in extracts diluted to concentrations indicated					
			Mean, all concentrations	.25	.1	.01	.001	.0001
Normal Kanred plants	Berkefeld	18	.008	.....	0	0	.....	.025
		19	.160	.....	.105	.182	.....	.192
	Filter paper	18	.031	.....	0	.027	.053	.042
		19	.154	.....	0	.250	.270	.096
	Centrifuged, then Berkefeld	18	0	.....	0	0	0	0
		19	.237	.....	0	.221	.296	.431
Kanred infected with form 18	Berkefeld	18	0	.....	0	0	0	0
		19	.246	.111	.....	.121	.286	.467
	Filter paper	18	.016	.....	.....	.006	.017	.025
		19	.059	.....	0	.063	.085	.086
Kanred infected with form 19	Berkefeld	18	.009	.....	0	.014	0	.022
		19	.110	.....	.037	.....	.077	.215
	Filter paper	18	.005	.....	0	.007	.002	.012
		19	.095	.....	.....	.013	.111	.161
Normal Mindum plants	Berkefeld	18	.012	0	0	0	.043	.018
		19	.108	.....	0	0	.352	.080
	Filter paper	18	.027	.....	0	0	.010	.097
		19	.042	.....	0	.038	0	.128
Mindum infected with form 18	Berkefeld	18	.007	.....	0	0	0	.026
		19	.154	.....	.128	.158	.127	.204
	Filter paper	18	.020	0	0	.041	.045	.016
		19	.140	.....	.069	.197	.170	.123
Mindum infected with form 19	Berkefeld	18	.045	0	.114	.026	.066	.019
		19	.203	.040	.269	.160	.453	.094
	Filter paper	18	.035	.....	.005	.021	.012	.100
		19	.107	.....	.006	.035	.192	.196

* Total lengths of branches divided by lengths of main germ tubes.

here are complex and certainly involve more than merely the development of branches instead of main germ tubes in "uncongenial" substrata.

Summary.—The growth from urediniospores of *P. graminis tritici* forms 18 and 19 was studied in hanging-drop cultures in extracts from normal Kanred and Mindum wheat plants, and from plants inoculated with the two rusts. Differentiation of growth of the forms, to which the varieties are reciprocally resistant and susceptible, in the extracts from normal plants confirmed the results of earlier experiments. The length of germ tube was greater in extracts from the diseased plants than in those from normal plants, and differences between the two forms also were intensified in the extracts from infected plants. Branching-ratio differentiation was not demonstrated so clearly in the extracts from diseased plants.

Some Characteristics of Differentiating Materials in Extracts

Stability in stored extracts:

Forms 18 and 19 in stored extracts.—Part of the extracts of lot 4 of Tables V to XV was stored in the refrigerator for eight months, in Pyrex tubes plugged with cotton, and then used in the preparation of hanging-drop cultures of forms 18 and 19. The stored material was diluted to one per cent in three different materials: plain one per cent agar; one per cent agar containing as nutrient 10 per cent of Shive's solution (20); and sterile, distilled water. The mean lengths of germ tubes as given in Table XXV have been corrected for variations in density of inoculum only. It is to be noted that the uncorrected figures showed precisely the same relations as those given here.

TABLE XXV.

DIFFERENTIATION OF FORMS 18 AND 19 OF *P. graminis tritici* IN KANRED AND MINDUM EXTRACTS PREVIOUSLY STORED IN THE REFRIGERATOR FOR EIGHT MONTHS

	Physiologic forms of *P. graminis tritici*	Extracts diluted to .01 in					
		Plain 1% agar		1% agar + 10% Shive's solution		Distilled water	
		Kanred	Mindum	Kanred	Mindum	Kanred	Mindum
Mean lengths of germ tubes, corrected for density of inoculum, in microns	18	481	304	316	218	367	299
	19	203	242	215	158	211	198
	18–19	278	62	101	60	156	101
Ratio, lengths of branches divided by lengths of germ tubes	18	.006	.002	.002	.007	.007	.003
	19	.031	.060	.009	.067	.015	.160
Production of apical swellings*	18	Trace	+	Trace	+	?	+
	19	?	Trace	+	—	Trace	?

* + = apical swellings present; ? = doubtful; — = absent.

As usual, forms 18 and 19 were clearly different on every substratum. Germ tubes of form 18 were longer in each case than those of form 19, but those of the latter branched more.

Comparing growth in Kanred substrata to that in the Mindum series, unusually consistent differentiation of forms to which the varieties are susceptible or resistant was obtained. In each of the three diluents form 18 germ tubes exceeded those of form 19 in length to a greater extent in the Kanred than in the Mindum cultures. Except for form 19 in the plain agar series, there was a higher production of the apical, teliospore-like bodies on germ tubes of each form in extracts from the resistant than from the susceptible plants. Contrary to results in previous series, however, branching ratios were greater in extracts from the susceptible variety than from the resistant one.

Refrigeration for eight months did not destroy the property in these extracts which differentiates forms to which the varieties are resistant or susceptible. In the present series, differentiation is clear using any one of three different materials with which to dilute the extracts, except that differentiation by branching ratios appears to have been reversed.

Forms 1 and 17 in stored extracts.—Such excellent differentiation was secured with forms 18 and 19 in the previous series that the same stored Kanred and Mindum extracts were used for cultures of forms 1 and 17. Kanred is immune and Mindum is moderately resistant to form 1, while Kanred is immune also from form 17 and Mindum is very susceptible to it. Stakman and Levine (30) symbolize these relations as follows:

	Kanred		Mindum	
Form	Range	Mean	Range	Mean
1	0 to 0;	0	0 to 2	1
17	0 to 1=	0	3− to 4++	4=

Data regarding the growth of these forms in the Kanred and Mindum extracts diluted to 0.01 in plain one per cent agar, and in plain agar checks, are given in Table XXVI. Lengths of germ tubes here were corrected for variations in density of inoculum as in Table XXV. Since form 1 produces the apical, teliospore-like bodies abundantly, the actual percentages of tips of germ tubes that produced these bodies were counted in the present series.

TABLE XXVI

Differentiation of Forms 1 and 17 of *P. graminis tritici* in Kanred and Mindum Extracts Previously Stored in the Refrigerator for Eight Months

	Physiologic forms of *P. graminis tritici*	Substrata		
		0.01 Kanred in plain agar	0.01 Mindum in plain agar	Plain agar checks
Mean lengths of germ tubes (corrected for variations in density of inoculum), in microns	1	79	141	258
	17	148	276	217
Ratio, length of branches over length of germ tubes	1	.010	.040	.042
	17	.158	.087	.106
Percentage of germ tubes producing apical swellings	1	86	27	38
	17	10	18	0

As would be expected, form 1 germ tubes were smaller in both of the much diluted extracts than in the checks. Moreover, germ tubes were shorter in the extract from the immune Kanred than in the extract from the very resistant Mindum. Also according to hypothesis, form 17 germ tubes were longer in the Kanred extract than those in the checks and smaller in the Mindum cultures than in the checks.

The results were as inconsistent as those of the preceding series with respect to the extent of branching and the production of apical swellings. Only the branching ratios with form 17, and the production of apical swellings with form 1, were as expected. As in Figure 7, D and B, some of the apical swellings produced by form 1 in the Kanred agar closely resembled teliospores, while those in the checks were fewer in number and of the more usual clavate shapes.

Considering both series, it is apparent that despite the lack of differentiation of all forms by all criteria, the characteristics of the four physiologic forms of *P. graminis tritici* when cultured on these extracts, eight months after extraction, were sufficiently different to indicate the actual variations in resistance of the wheat varieties to the four forms.

Stability to heating.—In Experiment 1 extracts made by processes involving cooking of any sort were of less value in differentiating forms by length of germ tubes than were extracts prepared without heating. From this it appeared possible that the materials which differentiate physiologic forms are thermolabile, or, if not, are affected by other results of the heating. However, in cultures in which extracts were diluted in plain agar, the extracts were held at 44.5° to 45.5° C., both when diluted and undiluted, for intervals often approaching two hours, apparently without lowering the differential value of the extracts. As a preliminary test, the experiment summarized in Table XXVII was performed. Cultures were prepared of Mindum extract diluted to 10 per cent in plain one per cent agar; this agar was then heated at

TABLE XXVII

Differentiation of Physiologic Forms of *P. graminis tritici* in 10 Per Cent Mindum Agar, in Cultures Prepared Immediately After Dilution at 45° C., and Others Prepared After Heating Agar at 97° C. for 15 Minutes

	Physiologic forms of *P. graminis tritici*	Growth in			Growth in Mindum agar minus that in checks	
		10% Mindum agar		Plain agar checks		
		Heated	Unheated		Heated	Unheated
Mean lengths of germ tubes (corrected for variations in density of inoculum), in microns	1	47	132	319	−272	−187
	18	30	197	363	−333	−166
	19	172	230	301	−129	−71
Ratio, length of branches over length of main germ tubes	1	0	.005	.004	−.004	+.001
	18	0	.008	.005	−.005	+.003
	19	.067	.048	.089	−.022	−.041
Percentage of germ tubes producing apical swellings	1	15	72	18	−3	+54
	18	9	15	0	+9	+15
	19	0	5	0	0	+5

97° C. for 15 minutes, cooled rapidly to 45° again, and a second series of cultures inoculated.

Mindum is resistant to forms 1 and 18, and susceptible to form 19. The results in the unheated agar are therefore in agreement with those of the previous experiments. Compared with the checks, mean lengths of germ tubes of forms 1 and 18 were much less than those of form 19. Branching ratios were slightly larger for forms 1 and 18 in the Mindum agar and considerably smaller for form 19 than in the corresponding checks. The production of apical swellings was increased markedly with forms 1 and 18. The only disagreement was in the slight increase in production of apical swellings with form 19 in the Mindum agar as compared to the check.

In the heated Mindum agar, growth was in general inhibited to a marked extent. Lengths of germ tubes were much shorter than in either of the other media; however, the average length of germ tubes of form 19 was still considerably more than that for either of the other two forms, and differentiation of the forms by the branching ratios was reduced but not lost.

It may tentatively be considered that those constituents in wheat extracts which can differentiate physiologic forms to which the variety is susceptible or resistant are probably not entirely destroyed by heating at 97° C. However, this heating reduces the value of the extract as a substratum for the rusts, and hence the differentiation may well be obscured in some heated extracts. From the results in Experiment 1, it seems possible that autoclaving may result in complete disappearance from extracts of the materials concerned in differentiation by lengths of germ tubes, with perhaps accentuation of the differentiation by the branching ratios.

Filtration methods as affecting differentiation.—In the experiment with extracts from normal and rusted Kanred and Mindum plants, a portion of each extract was filtered through a single filter paper and another portion ultrafiltered through a Berkefeld filter. The summarized results as to lengths of germ tubes for forms 18 and 19 in these extracts are given in Table XXIII. Correct differentiation here is indicated by positive values in the Kanred series and negative values in the Mindum series. It will be noted that there was greater differentiation in the extract filtered only through filter paper in every series except the Mindum infected with form 19. Averaging all values in the table, the relation is marked:

	Kanred series	Mindum series
ultrafiltered	14μ	7μ
filtered through paper	77μ	—67μ

Differentiation by length of germ tubes was undoubtedly more pronounced in the rather turbid green filtrate which passed through filter paper than in the clear ultrafiltrate in this series. The differentiating materials may be located in the chloroplasts, which would agree with the conception that growth of rusts is intimately connected with photosynthesis of the host. It would be equally plausible, however, to consider that differentiation in elongation may be due to completely soluble materials, present equally in both filtrates; but that differentiation may be magnified in the presence of additional purely nutritive and non-differentiating materials in the chloroplasts, or otherwise contained in greater concentration in filtrates through filter paper.

In the same ultrafiltered and paper-filtered extracts, the differences in branching ratios were intensified in the ultrafiltrates, since form 19 ratios were larger in them and the form 18 ratios usually smaller. Differentiation by branching ratios is possibly the result of materials or conditions in the extracts other than those concerned in the differentiation by lengths of germ tubes.

Tests of the Production of Toxins by Rust Sporelings

Varietal resistance to physiologic forms of rusts is probably due to either, or conceivably both, of the following general relations: (1) variations in the nutritive value of the host to the parasite; and (2) variations in the actual resistance of host varieties to the toxic activities of the different physiologic forms. The former hypothesis is the one on which most of the experiments in the present paper have been planned, but some preliminary tests of the latter hypothesis also are given.

The second hypothesis may be considered to involve, essentially, the ability of susceptible host tissues to tolerate such toxic materials as may be excreted by the parasite or produced by the host under stimulation from the parasite. All other tissues, resistant or immune, will not tolerate or withstand these hypothetic toxic materials, so that host cells in the vicinity of the point of infection die; the typical "hypersensitive area" is produced; and the parasite, thus cut off from its living nutrient substratum, soon dies also.

If this hypothesis is correct, it might be possible to demonstrate its probability by exposing various host tissues to the action of liquid media in which rust spores have grown. Resistant plants, if actually more susceptible to the toxic substances, should suffer greater injury than susceptible tissues. Direct determination by somewhat similar methods of the production by plant pathogens of materials toxic to the host tissues has been successful with various species of *Fusarium*, following the work of Haskell (11) and of Fahmy (9) with *Fusarium* *solani.* So far as the writer knows, there is no previous record of this type of experiment with rusts.

Hypodermic Injection of Culture Filtrates

Mass sowings of urediniospores of *P. graminis tritici* forms 14 and 27 were made in an extract, from normal Kanred wheat plants, which was diluted in sterile, distilled water to .01 concentration and used 5 cc. per culture in Erlenmeyer flasks. Three flasks were used for each form. The cultures were incubated at 23° C. for three days and the liquid was then filtered through sterile filter paper, using aseptic precautions, to remove the thin surface films of spores and germ tubes. Composite samples of the filtrates for each form were injected into the stems of 17-day-old wheat seedlings. Ten plants each of Marquis, Mindum, Speltz Marz, and Vernal emmer were used for each of the culture composites and for the check filtrate from the uninoculated blanks.

Injections were by means of finely drawn glass tubing with tips of approximately .2 mm. outside diameter and .15 to .16 mm. inside diameter. As much liquid as possible was forced into the stems, leaving always a drop of the liquid standing over the puncture as the needle was withdrawn. Only a slight amount of liquid appeared to be retained in the punctures. Each plant was injected at two or three points between the first and second nodes above ground. The plants were kept in the greenhouse as before injection.

Observations were made for three weeks. Six days after the injections definite but very narrow brownish necrotic halos, probably due to the mechanical injury, appeared around all of the punctures. No further injury developed, nor were there any differences between varieties or between the culture and check-filtrate injections in the extent of the injury.

Absorption of Culture Filtrates

The negative results of the previous experiment might be attributed to the fact that too little of the liquid was introduced to cause injury. In further tests, portions of the same culture filtrates were used again, but in such a way as to introduce larger quantities into the plants.

Wheat seedlings grown 18 days in the greenhouse were cut off at the surface of the ground, rinsed immediately in distilled water, and the stems cut back again while still in the water. The plants were placed immediately in individual small glass tubes, of 4 mm. outside diameter, 6.5 cm. long, and sealed at the bottom. The tubes, previously filled nearly to the tops with filtrates, or with sterile, distilled water in the case of checks, were then supported in cardboard racks on the greenhouse bench. As the various liquids were taken up by the plants, sterile, distilled water was added from time to time to keep the tubes almost full. Thus, irrespective of the rate of imbibition, each plant eventually absorbed approximately the same amount of the original solution as did the others.

The results were decisively negative. Plants treated as described lived for three days to a week in different series. The form 14 filtrate was tried with Marquis, Khapli, Little Club, and Vernal emmer wheat seedlings; and the form 27 filtrate with Marquis and Khapli seedlings. In each case both check filtrates from uninoculated blanks and distilled water were used for comparison. The type of liquid appeared to have not the slightest influence on the prolongation of greenness or turgidity or on the prevention of wilting. All plants of the same variety showed the same gradual decline and death, differing in time for the different varieties, regardless of their differing substrata.

The results indicate either that the fungus does not produce materials toxic to wheat tissues, or that the methods used were not adequate to demonstrate such materials. In any case, no toxic activity by the fungus was shown. This agrees with the results previously discussed, which indicate that physiologic resistance can be explained by differences, in the normal plant constituents, which affect the growth of the various physiologic forms of *P. gramminis tritici.*

DISCUSSION

Considerable differences were found in the growth of uredinial germ tubes of different physiologic forms in hanging-drop cultures of water, plain agar, and other substrata (Fig. 1). These differences were consistent, and indicate that physiologic forms of *P. graminis tritici* may be differentiated, in hanging-drop cultures under specified conditions, by the type of growth, the length of germ tubes, and the relative abundance of branches on the promycelium, in much the same way as physiologic forms of other fungi (6, 8) have been identified by cultural characteristics. It must be noted, however, that the present work has not shown whether the differences found between forms of *P. graminis tritici* are true of all isolations of a given form, or are characteristic merely of those studied. More than one isolation of a given physiologic form was rarely studied in this investigation. In preliminary comparison of two isolations of form 39, there was rather close agreement of characteristics in drop culture; but many more isolations must be studied before it can be concluded that the characteristics observed in drop cultures always correspond with pathogenic characteristics.

The foregoing statement does not apply to the relation between the rate of production of apical swellings and the host range of physiologic forms of *P. graminis tritici.* There seems to be a positive correlation between the readiness with which these teliospore-like bodies are produced and the narrowness of host ranges of the forms.

It appears unlikely that the production of apical swellings bears a direct causal relation to the restriction of host range with which it appears to be associated. We may, however, consider it tentatively as an indication of those physiologic potentialities of the fungus which are concerned in resistance. Thus, if mycelium from germinating urediniospores tends to enter almost immediately a reproductive stage which inhibits further vegetative growth, and this tendency varies in intensity in different physiologic forms, then for a particular form the percentage of germ tubes that produce apical swellings under specified conditions may serve as an index of the intensity of this tendency toward reproduction. To complete this hypothesis, we may assume further that physiologic forms that produce many apical bodies, and in which the "reproductive" tendency is accordingly high, the host range is relatively restricted because the conditions required for successful vegetative growth are more highly specific than those necessary for the growth of physiologic forms that produce fewer apical swellings.

A converse relation may also be deduced from this correlation. If the production of apical swellings is an index to extensiveness of host ranges, it would appear from the correlation that the twelve varieties selected by Stakman and Levine as representative of wheat varieties were correctly chosen.

It is in accord with our general idea of the complex nature of physiologic resistance that it should be true that the correlation between the percentages of germ tubes that produce apical swellings and the extent of the host ranges of the forms is not applicable to the entire population of physiologic forms studied. The correlation applies to the majority of physiologic forms, but apparently does not hold for form 39 and several forms to which Vernal emmer is susceptible. These same forms were again found to be the only ones aberrant in other respects, as reported elsewhere in this paper. In studying the growth of physiologic forms in extracts from susceptible and resistant plants, it was found that differences in cultural characteristics of all forms studied corresponded with differences in pathogenicity except with form 39 and those forms to which Vernal emmer is susceptible. Were these discrepancies not confined to a definite group, they might constitute a serious objection to the general idea that the drop-culture characteristics studied in this paper are to be considered evidence of the physiologic interrelations of host and parasite which may be concerned in physiologic resistance to rusts. As it is, from the consistent way in which these same forms were aberrant to the various types of results, the writer would instead consider the following explanation more probable.

A series of relations concerned in resistance to most physiologic forms of *P. graminis tritici*, but perhaps not extending to the Vernal-emmer group, which may for convenience be considered to include form 39 also, may be demonstrated in artificial culture by the growth of the physiologic forms in extracts. The Vernal-emmer group is possibly included in this group so far as physiologic resistance in the plant is concerned; but demonstration of the relation in drop-culture growth is masked perhaps by differences in environmental characteristics. It would be equally plausible, however, to consider that some factors involved in resistance to the Vernal-emmer group are important only with that group, and are of little or no importance in resistance to the other physiologic forms that are affected primarily by the relations demonstrable in culture. The writer has no explanation to offer for the fact that form 39 so persistently and clearly resembles the Vernal-emmer series, altho this variety is so resistant to form 39. It is evident that the basis for the reactions in artificial culture of the forms constituting this group – distinguished, it is to be remembered, merely by aberrancy—is not the same as that which enables a form to parasitize Vernal emmer successfully.

The most significant results of this work appear to be those bearing on the nature of resistance of wheat varieties to *P. graminis tritici*. Physiologic resistance to stem rust appears to be based at least in part on the composition of the normal host cells, entirely in the absence of any infection. Despite the slight mycelial growth obtained from urediniospores in hanging-drop cultures of even susceptible varieties, there were constant differences between the growth of the physiologic forms which agreed with the susceptibility of the varieties to the forms. In extracts from plants susceptible to a given form, germ tubes were in general longer than in check cultures; while in extracts from resistant plants, the germ tubes were shorter than in the checks. Germ tubes branched more and produced a higher percentage of apical swellings in extracts from resistant plants than in those from susceptible plants, altho these differences did not occur regularly with the aberrant physiologic forms of the Vernal emmer group.

These differences in germ tube growth in the various extracts, diagnostic of the resistance relation of the forms to the varieties, appeared consistently in extracts prepared from normal plants. In one experiment the differentiation was intensified in extracts prepared from infected seedlings. This may indicate some antibody formation, altho extraction from infected or dead cells of inoculated plants may be more thoro and merely furnish a higher yield of materials concerned in resistance, which are also present in the normal tissues.

The results indicate that physiologic resistance is caused by the inability of the fungus to survive in tissues of resistant plants, an inability based on the composition of the normal tissues. Whether it is due to the presence in susceptible tissues of specifically nutritive materials which are absent in resistant tissues, or to the presence in resistant tissues of toxic materials absent in the susceptible tissues, cannot be determined with the information at hand. Either aspect of the hypothesis assumes that injury to the tissues of resistant host plants comes from the toxic materials given off by the dying or dead fungus cells in the uncongenial resistant tissues. It may be noted that in other cases in which the basis of physiologic resistance has been explained as due to differences in the composition of the normal host plants Walker (32) has considered that resistance to onion smudge is due to the presence of specific toxic substances in the scales of resistant onions, and Reynolds (24) has suggested that resistance to *Fusarium lini* is based on greater concentrations of glucosides in the resistant flax plants.

Whether the materials concerned in physiologic resistance, and serving also to differentiate physiologic forms in extracts from the plants, are primarily in the resistant plants, the susceptible ones, or both, it is clear that they are effective in considerable dilution. Approximately the same relations between physiologic forms were shown in the present work in dilutions of extracts to .001 or .0001 as in the most concentrated solutions in which successful growth could be secured. Extracts stored in the refrigerator for eight months were still capable of differentiating forms to which the varieties are resistant or susceptible, whence it would appear that the materials concerned are relatively stable. In Experiment 1, extracts prepared by heating did not differentiate physiologic forms so clearly by the differences in lengths of germ tubes as extracts prepared without heating; yet differentiation was still possible in series of cultures prepared (Table XXVII) with extracts which, after being mixed with the agar diluent, had been heated to 97° C. for 15 minutes. Differentiation by lengths of germ tubes was more definite in extracts filtered only through filter paper rather than through the Berkefeld filter; while differentiation by differences in the branching ratios was more definite in the ultrafiltrates. Apparently more than one series of materials is concerned in differentiation by these various cultural characteristics, unless one of the characteristics is affected by much more dilute concentrations of the host materials than is the other.

Further investigation of this sort, in which the living sporelings are used as indicators of the results obtained by fractionations of plant extracts, should yield a more accurate idea of the materials actually involved in resistance to rusts and perhaps also of those utilized in their nutrition.

SUMMARY

1. The growth from urediniospores of *Puccinia graminis* was studied in hanging-drop cultures. Growth beyond about 1,000 μ was seldom obtained. Cultural characteristics, such as length of germ tubes, the type of growth, and abundance of branching, differed in these sporelings with different physiologic forms of *P. graminis tritici,* tho these characteristics are constant for given strains under controlled conditions. It has not yet been proved whether these cultural characteristics are true of all isolations of the physiologic forms, or are characteristic merely of particular strains within them.

2. There is high positive correlation between the number of urediniospores with which a drop is seeded and the final length of germ tube per spore. This has been worked out for many forms of rusts and for a number of substrata. The increase in length of germ tubes with increased density of inoculum is great enough so that corrections were calculated and applied, to insure that conclusions based on differences in lengths of germ tubes would not be influenced by the unavoidable differences in density of inoculum in the experiments.

3. Apical swellings on the tips of germ tubes, regarded as occasional or abnormal by earlier workers, were produced by all forms of all species studied to any considerable extent. These bodies resemble teliospores morphologically, are produced by different physiologic forms of *P. graminis tritici* in approximately the same relative abundance as normal teliospores on infected wheat plants, and are probably immature teliospores. The production of apical, teliospore-like bodies is negatively correlated with the number of spores per drop.

4. Teliospore-like bodies are produced by the physiologic forms of *P. graminis tritici* under identical conditions on a purely synthetic medium—plain one per cent agar—at rates relatively constant per form and widely varying between forms. The rates vary in linear correlation with the extensiveness of the host (variety) ranges of the forms, for almost the entire population of physiologic forms tested. Percentages of germ tubes producing teliospore-like bodies are higher in artificial cultures of forms with relatively limited ranges and progressively lower with physiologic forms of more extensive host ranges. A definite group of forms of *P. graminis tritici,* including form 39 and those of the forms tested to which Vernal emmer is susceptible, are aberrant to the linear correlation noted.

5. Extracts prepared from wheat varieties differed in their ability to support the growth of physiologic forms of *P. graminis tritici* in exact agreement with the respective resistance or susceptibility of the varieties to the various forms. Congeniality of forms to host varieties was evidenced almost universally by greater lengths of germ tubes in extracts from susceptible varieties, less branching, and lower production of apical swellings, than in extracts from resistant varieties. All forms of *P. graminis tritici* tested fit the groupings of resistance by their reactions in culture to host extracts, except those forms to which Vernal emmer is susceptible and form 39, the same group that was aberrant to the linear correlation. Evidently there are at least two series of relations involved in resistance to *P. graminis tritici*, unless these aberrant forms differ from the majority in some minor environmental responses that interfere with cultural results without affecting the relation between the parasites and their hosts.

6. In a single experiment, differentiation was greater with extracts from inoculated plants than in extracts from normal plants. Antibody activity may be, but is not necessarily, involved.

7. Extracts stored in the refrigerator for eight months still contained materials that differentiated between forms to which the variety concerned is susceptible or resistant. Extracts prepared by methods involving heating apparently did not contain the materials affecting germ tube elongation. A partial sterilization of extracts by filtration through a single, sterile filter paper instead of the usual filtration through a Berkefeld filter produced substrata of greater differentiating activity as to lengths of germ tubes, but of less differential value with regard to differences in the branching of germ tubes.

8. Materials extractible from normal as well as infected wheat tissues are able to affect the growth of physiologic forms of *P. graminis tritici,* in artificial culture in the extracts, in a manner diagnostic of the resistance of the host to the various physiologic forms. These materials in the plant tissues presumably explain the phenomenon of physiologic resistance to stem rust.

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Inheritance Studies in Phaseolus Vulgaris

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CONTENTS

Page

Review of literature 3

Methods of studying the lignified cells of the pod sutures 4

  A cross between Wardwell (stringless) and Longfellow (stringy) 7

  A cross between Pencil Pod (stringless) and Robust (stringy) 8

  A cross between Refugee Wax (stringless) and Tennessee Green Pod (stringy) 9

Inheritance of fiber in the side wall of the pod 13

Inheritance of width of pods 17

Linkage relations 21

Studies on pod color 22

Summary and conclusions 26

Bibliography 27

INHERITANCE STUDIES IN PHASEOLUS VULGARIS[1]

T. M. CURRENCE

The development of the snap bean as a canning crop and as a fresh vegetable has served to emphasize the importance of certain pod characters. The canning trade, especially, is insistent that the pods of a variety meet certain requirements of shape, size, color, tenderness, and uniformity. While a number of genetic studies have been made on the bean plant they have for the most part failed to include pod characters. Where pod characters have been worked with, the results have been somewhat indefinite and unsatisfactory. In an attempt to clarify and extend the genetic information on some of the important characters of the pod, the studies composing this paper were made. The characters chosen are lignified tissue in the sutures and in the side walls, the shape of the pod in cross-section, and color of the pod as related to localized chlorophyll development.

REVIEW OF LITERATURE

A number of workers have reported on the inheritance of strings in the bean pod. The majority have considered the presence of strings to differ by a single genetic factor from the absence of them. Stringlessness has been largely considered the dominant allelomorph. Emerson (1904) submitted data indicating a single-factor relationship in certain crosses, but also data from other crosses which could not be readily explained on this basis if the classifications were properly made. The second type of result reported by Emerson gave an intermediate F_1, and an excess of stringy type in F_2. Progeny of stringless, intermediate, and stringy F_2 plants gave segregation in F_3. In other crosses the stringy character did not segregate in F_3. Tschermak (1916) reported results much the same as those of Emerson's and considered stringlessness dominant. A part of his data could not be explained by a single-factor difference. More recently Wellensiek (1922) reported data that support the single-factor hypothesis but he did not have an F_3 generation to verify his conclusion. His F_2 was grown from three different crosses and was made up of 191 plants. The results closely approximated the three stringless to one stringy expectation. Joosten (1927) reported rather extensive studies of the morphological structure of the string. He stated that the string is composed of a group

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[1] This paper was also submitted to the faculty of the Graduate School of Cornell University in partial fulfillment of the requirements for the degree of doctor of philosophy.

Grateful acknowledgment is made to Dr. R. A. Emerson for valuable help in starting this study and for the helpful suggestions given during the course of the work.

of schlerenchymous cells that form the cap of the fibrovascular bundles. A certain positive relationship was found to exist between the degree of lignification of these cells and the strength of the string when removed. Joosten suggested that an entirely stringless variety probably does not exist and that maturity of pods and environment greatly affect the degree of stringiness. He submits data which are not in agreement with the single-factor hypothesis and believes the genetic relationship to be a complex one.

Tschermak (1916) studied the inheritance of pod shape in a cross of round by flat. His data suggested round to be dominant, or nearly so, and a complicated segregation to occur in the F_2 generation.

Woycicki (1927) reported on the inheritance of breadth and thickness of pods and also the ratio between the two characters. The studies were made on two crosses of three different varieties. In both crosses the width was considered as a two-factor difference. In one of the crosses the thickness was also caused by two factors. In the second cross there was not a significant difference between the thickness of the parents, but in F_3, certain lines appeared that apparently were distinctly different for thickness. When the ratio of width to thickness was taken there appeared to be three or four cumulative factors. By segregating different combinations of factors for width and thickness, lines were obtained that were flatter and more round than either parent.

Pod color has been studied by several workers; Emerson (1904) and Tschermak (1916) found the green type dominant to yellow and a ratio approaching three green to one yellow in the second generation. F_3 results also were in agreement with those expected from a single-factor difference. The silver color of the Crystal-White Wax variety has not been studied, altho the variety was used by Halsted (1907) in crossing work. He failed to distinguish the double recessive type from the ordinary yellow, and made no report on the various proportions of the different colors which segregated.

METHODS OF STUDYING THE LIGNIFIED CELLS OF THE POD SUTURES

A microchemical test for lignin seemed to be the most accurate method of determining the presence or the absence of schlerenchymous tissue in the pod sutures. The method of breaking the point of the carpel and attempting to pull out the string has certain advantages, but is somewhat unreliable for making accurate classification. Especially is this true if more than two phenotypes are wanted. The chief objection to using the microchemical test is the time required to cut and examine the sections. This was found to limit the number of plants that could be studied.

The analine sulphate test for lignified cells was found to distinguish very sharply between the stringy and stringless types when applied to the parental material. The test reacts on lignified tissue to give a very bright yellow color to sections from stringy pods. The sections from the stringless parent were stained by the test, but the color was a dark brown and was readily distinguished from that of the stringy parent.

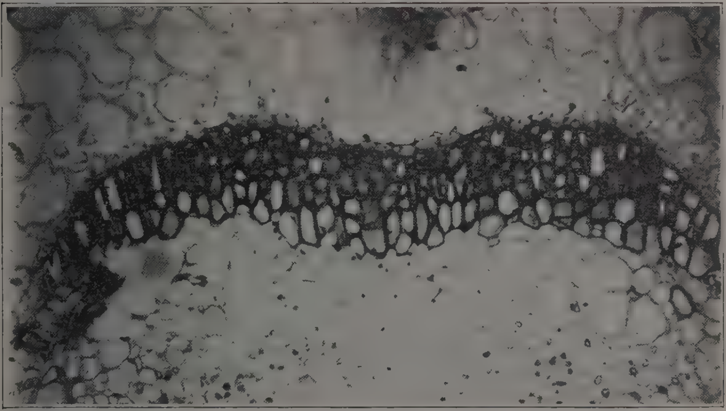

Fig. 1. Transverse Sections of the String Area of the Stringless Type
The groups of dark stained cells are the strings. Enlargement about 280 times.

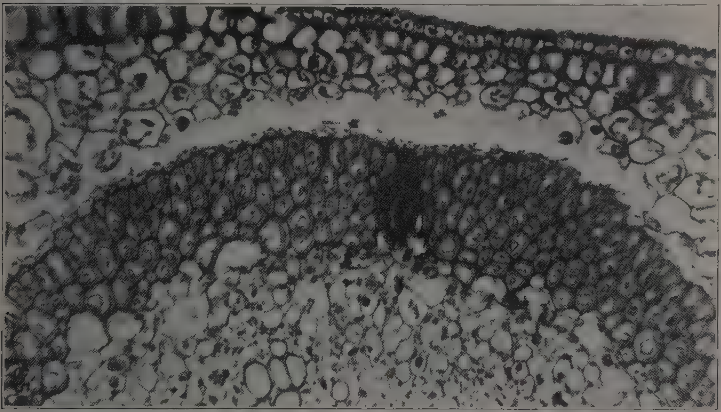

Fig. 2. Transverse Sections of the String Area of the Stringy Type
The groups of dark stained cells are the strings. Enlargement about 280 times.

Anatomically the string appears to be the cap of the fibrovascular bundles in the sutures of the pod. The cap is present in the stringless type of beans but the cells do not take on the thickened lignified nature that characterizes the stringy type. When the hybrids were classified, a single pod was taken as representative of the plant. Tests made on a stringy variety indicated only a slight reduction in variability when two or four pods per plant were used and averaged instead of a single-pod sample. The approximate area of the tissue that gave a positive reaction to the test was measured by an ocular micrometer, and the results were expressed in square millimeters. Stringless plants are considered to be those with an area of less than .005 square millimeter. The terms "stringy" and "stringless," therefore, are used to designate these groups.

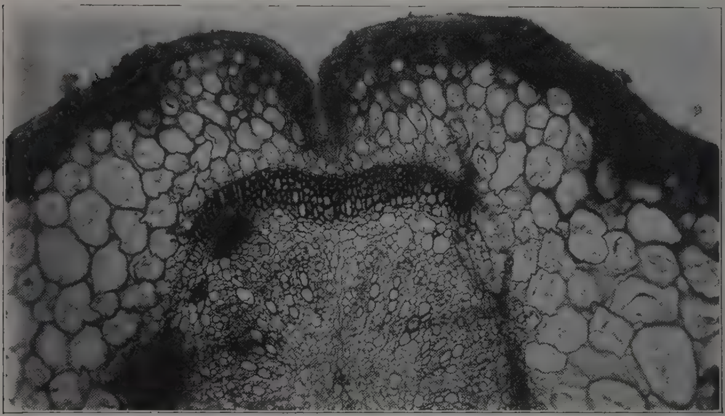

Fig. 3. Lower Magnification of Transverse Sections of the String Area of the Stringless Type

Note fibrovascular bundles located under the strings. Enlargement about 115 times.

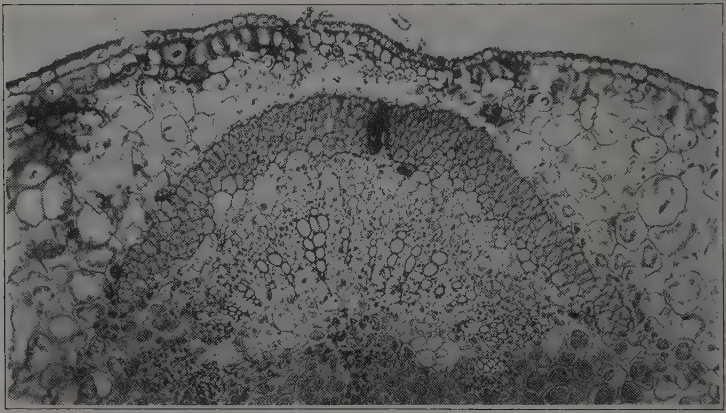

Fig. 4. Lower Magnification of Transverse Sections of the String Area of the Stringy Type

Note fibrovascular bundles located under the strings. Enlargement about 115 times.

The sections were cut from the region between the first and second seeds from the tip of the pod. The measurements mentioned are for half of the string inasmuch as the pods were separated at the sutures and placed in pith to cut the sections. Data from three crosses were obtained through the F_3 generation. These and other crosses will be taken up separately.

A Cross Between Wardwell (Stringless) and Longfellow (Stringy)

The F_1 of this cross consisted of 4 stringless plants and the F_2 was made up of 67 stringless to 33 stringy plants. In determining the breeding behavior of the F_2 plants, the same method of staining and measuring the lignified area was continued. If all the progeny from a single plant gave measurements of less than .005 square millimeter, that plant was considered as breeding true for "stringless." F_2 plants giving all progenies with an area of .005 or greater were considered as homozygous "stringy," and progenies whose measurements included both these groups were classified as being from F_2 plants heterozygous for the string character. The third generation data for this cross are given in Table I.

TABLE I

F_3 PROGENY OF RANDOM SELECTIONS OF F_2 INDIVIDUALS CLASSIFIED AS STRINGLESS AND STRINGY, WARDWELL × LONGFELLOW

Genotype	F_2 stringless plants	F_3		Genotype	F_2 stringy plants	F_3	
		Stringless	Stringy			Stringless	Stringy
Homozygous stringless	1	14	0	Heterozygous	1	2	4
	2	2	0		2	2	3
	3	15	0		3	4	17
	4	12	0		4	13	21
	5	11	0	Homozygous stringy	5	0	8
	6	23	0		6	0	16
	7	17	0		7	0	11
	8	6	0		8	0	9
	9	5	0		9	0	13
	10	12	0		10	0	8
Heterozygous	11	7	2		11	0	10
	12	3	3		12	0	20
	13	2	4		13	0	20
	14	18	4				
	15	5	5				
	16	15	3				
	17	13	7				
	18	8	3				
	19	1	4				
	20	13	16				
	21	14	8				
	22	10	3				
	23	1	11				
	24	3	4				
	25	7	18				
	26	9	4				
	27	3	11				
Homozygous stringy	28	0	10				
	29	0	3				

Twenty-nine progenies were grown from the stringless F_2 group. Ten were stringless, 17 segregated, and 2 were stringy. It should be stated that the ratio of stringless to stringy in the segregating F_3 populations is thought to be of limited significance as the genotypic test of the F_2 shows the error involved in dividing the 2 phenotypes. At least 2 of the F_3 populations from the stringless F_2 group (numbers 2 and 29) are undoubtedly too small to give accurate results. If these 2 lines are excluded, the figures are: 9 breeding true for stringless, 17 segregating, and one breeding true for stringy. If all the 67 F_2 individuals of this class are divided in these proportions, the result is 22.3 homozygous stringless, 42.2 heterozygous, and 2.5 homozygous stringy. As none of the F_3 population from stringy F_2 plants tested were extremely small, they are all included in the calculations. Four of the 13 segregated and the remaining 9 bred true for stringy. This is considered to indicate that 4/13 of the F_2 stringy plants were heterozygous and 9/13 were homozygous stringy. The 33 plants divided in these proportions give 10.2 heterozygous and 22.8 homozygous stringy. These figures combined with those obtained from the stringless give 22.3 plants homozygous stringless, 52.4 heterozygous, and 25.3 homozygous stringy. Altho the phenotypes could not be finely divided, the results from testing the genotypes suggest a single genetic-factor difference. This hypothesis calls for the three genotypes to be present in F_2 in a ratio of 1:2:1; or in this case, 25 homozygous stringless, 50 heterozygous, and 25 homozygous stringy. The P value for the results secured is .84 which means a chance deviation as great as this would be expected eighty-four times in one hundred such trials.

A Cross Between Pencil Pod (Stringless) and Robust (Stringy)

The F_1 of this cross consisted of 6 plants, all of which were stringless. In F_2 there were 157 stringless and 87 stringy plants. Table II gives the F_3 results. Progenies from 10 stringless F_2 plants were grown. Five were entirely stringless and 5 were apparently from plants heterozygous for strings. Dividing the 157 F_2 stringless plants in this proportion gives 78.5 homozygous stringless and 78.5 heterozygous.

Fourteen stringy F_2 plants gave progenies the following generation. Five were homozygous stringy and 8 heterozygous. The 87 stringy F_2 plants in this proportion are 37.3 and 49.7, respectively. Figures for the two F_2 groups combined show the 3 genotypes to be 78.5 homozygous stringless; 128.2 heterozygous; 37.3 homozygous stringy. This is quite a wide deviation from a theoretical ratio of 1:2:1. It may be explained, however, by the possibility that certain of the F_3 lines may be wrongly classified. That this possibility is not a remote one may be noted from the F_3 results given in Table II. If larger F_3 populations were available, certain of the lines would probably be found in other groups.

TABLE II

F_3 Progenies of Random Selections of F_2 Individuals Classified as Stringless and Stringy, Pencil Pod × Robust

Genotype	F_2 stringless plants	F_3 Stringless	F_3 Stringy	Genotype	F_2 stringy plants	F_3 Stringless	F_3 Stringy
Homozygous stringless	1	6	0	Heterozygous	1	3	3
	2	13	0		2	22	19
	3	7	0		3	2	3
	4	7	0		4	5	21
	5	7	0		5	4	11
Heterozygous	6	8	7		6	10	6
	7	21	7		7	7	14
	8	15	1		8	5	7
	9	31	15	Homozygous stringy	9	0	23
	10	47	9		10	0	32
					11	0	28
					12	0	12
					13	0	23
					14	0	14

Different classification of a very few lines would greatly change the results, as each group is represented by a small number of F_3 populations.

	Homozygous stringless	Heterozygous	Homozygous stringy
Observed	78.5	128.2	37.3
Calculated 1:2:1	61	122.0	61.0
Difference	17.5	6.2	—23.7

A Cross Between Refugee Wax (Stringless) and Tennessee Green Pod (Stringy)

The data from this cross appear to be markedly different from the two previous crosses, and cannot be readily explained by a single-factor hypothesis. The F_1 of this cross is distinctly stringy; an excess of stringy also occurs in the F_2 grouping. The F_2 population was made up of 19 stringless and 64 stringy. The F_1 consisted of 3 stringy plants. As indicated in Table III, 11 stringless F_2 plants produced progeny—4 were entirely stringless and 7 segregated into both types. Of the 37 stringy F_2 plants that produced progenies in F_3, 19 were heterozygous, 17 bred true for stringy, and one produced only stringless. The figures are considered to indicate that the 83 F_2 plants were made up of the 3 genotypes in the following proportions: 8.3 homozygous stringless, 44.3 heterozygous, and 29.4 homozygous stringy. The hypothesis which may best explain these figures calls for theoretical numbers of 5.2 homozygous stringless, 41.5 heterozygous, and 36.3 homozygous stringy. The P value is approximately .19. Altho this value is rather low to be considered generally significant, the nature of the present data are such that it may be of importance. Small populations and possible errors in classifying the material might tend to detract from the agreement between the theoretical and actual ratios.

TABLE III

F_3 PROGENIES OF RANDOM SELECTIONS OF F_2 INDIVIDUALS CLASSIFIED AS STRINGLESS AND STRINGY, REFUGEE WAX × TENNESSEE GREEN POD

Genotype	F_2 stringless plants	F_3		Genotype	F_2 stringy plants	F_3	
		Stringless	Stringy			Stringless	Stringy
Homozygous stringless	1	11	0	Homozygous stringless	1	8	0
	2	5	0				
	3	12	0	Heterozygous	2	3	5
	4	4	0		3	3	7
Heterozygous	5	7	4		4	3	1
	6	10	1		5	4	4
	7	20	4		6	3	4
	8	3	1		7	7	4
	9	11	7		8	1	7
	10	13	6		9	4	10
	11	5	2		10	5	8
					11	1	7
					12	11	4
					13	3	8
					14	1	4
					15	4	11
					16	1	8
					17	7	1
					18	3	23
					19	1	15
					20	1	11
				Homozygous stringy	21	0	6
					22	0	10
					23	0	7
					24	0	16
					25	0	11
					26	0	8
					27	0	2
					28	0	7
					29	0	11
					30	0	13
					31	0	14
					32	0	12
					33	0	5
					34	0	14
					35	0	13
					36	0	18
					37	0	17

The hypothesis for explaining the data from the 3 crosses assumes one dominant factor producing stringless, but a second factor, when present, inhibits the action of this factor. The factor for stringless is indicated by S and the inhibiting factor is termed T. Assuming these 2 factors it is possible to have 3 genetic types of stringy, namely TTSS, TTss, and ttss; whereas the only possible stringless is ttSS. A cross of

TTss by ttSS would give a phenotypic ratio of 13:3 or a genotypic one of 1:8:7. This is a possible combination for the Refugee Wax × Tennessee Green Pod cross. A cross of ttSS by ttss would give results such as those obtained in the first two crosses discussed.

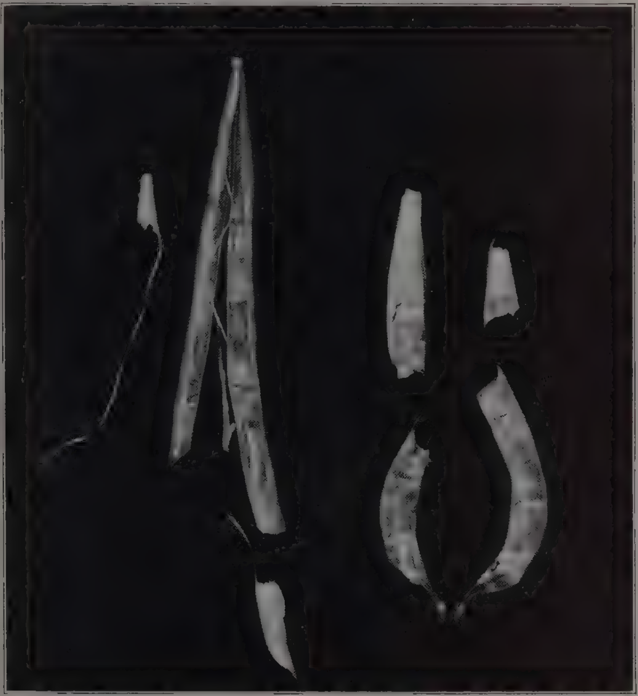

Fig. 5. Pods of the Stringy and Stringless Types

Emerson's data (1904) which did not seem to conform to the hypothesis of a single dominant factor for stringless may possibly be brought into agreement with the data of this paper. Emerson's data for the cross wherein he found dominance to be incomplete are as follows: 10 F_3 lines were grown from stringless F_2 plants; 5 of these bred true and 5 segregated; 7 of the intermediate F_2 class were tested and all were found to segregate; 11 stringy F_2 plants produced progeny; 7 of these bred true for stringy and 4 were heterozygous. Applying these proportions to the F_2 of Emerson's 5 crosses with a population of 114 stringless, 80 intermediate, and 78 stringy, gives the following:

	Homozygous stringless	Heterozygous	Homozygous stringy
Observed	57	165	50
Calculated 1:2:1	68	136	68
Difference	—11	29	—18

P value equals .001.

Thus Emerson's data may roughly agree with the expected results if the crosses were between TTSS and ttSS. That the agreement between the actual and theoretical is very poor is realized, but the difficulties of classifying the material and the combining of data from 5 different crosses are of importance in this connection. There is an important possibility that some of these crosses were between TTss and ttSS. This combination would give dihybrid results and therefore might cause the poor agreement. Unfortunately, the data from Emerson's individual crosses are not available.

The figures in Table IV from a number of additional crosses provide some evidence that may be of interest. These data were obtained by pulling out the string of mature pods and classifying them as either stringless or stringy. Altho the value of these figures is limited by the fact that only phenotypic ratios are available, one point is rather definitely demonstrated and at least one other is suggested. It is fairly definitely shown that the stringlessness of the variety Refugee Wax is genetically different from that of certain other varieties and it is suggested that two genetic types of stringy may also exist.

TABLE IV

F_1 and F_2 Data on the Inheritance of Strings from Crosses between Various Varieties

Varieties crossed	Designation number of cross	F_1	F_2		Possible theoretical ratio	Deviation
			Stringless	Stringy		
Burpee's Stringless × Davis Wax (stringy)	1	2 stringless	21	7	3:1	0
Burpee's Stringless × Black Valentine (stringy)	2	2 stringy	57	69	7:9	1.9 ± 3.76
Refugee Wax (stringless) × Longfellow (stringy)	3	Unknown	15	47	1:3	0.5 ± 2.30
Refugee Wax × Black Valentine	4	3 stringy	7	17	1:3	1.0 ± 1.43
Refugee Wax × Crystal White Wax	5	2 stringy	13	80	3:13	4.47 ± 2.54
Crystal White Wax × Refugee Wax	6	Unknown	26	152	3:13	7.4 ± 3.51

A single Black Valentine (stringy) plant was crossed with the two stringless varieties, Burpee's Stringless Green Pod and Refugee Wax. As indicated in Table IV, the result approaches a ratio of 7 stringless to 9 stringy in one case and in the other the observed result closely agrees with a 1:3 ratio. The crosses referred to are numbers 2 and 4. It is believed that the difference is too great to be explained on the basis of inaccurate classification of the F_2 plants. This is in disagreement with the theory used to explain the F_3 results, previously discussed, inasmuch as that hypothesis required that all stringless plants be of the same genetic constitution for stringless. It is apparent that the two ratios in Table IV may be explained by assuming two dominant complementary factors necessary for the development of strings. It may be considered that Black Valentine carries both factors, Refugee Wax one, and Burpee's Stringless Green Pod neither of them. But to bring this hypothesis into agreement with results from other crosses requires the assumption of at least two additional factors. Such an explanation is probably too theoretical to be justified without more extensive data than is now available.

That two genetic types of stringy exist is suggested by crosses 1 and 2. Burpee's Stringless was used as the stringless parent in both crosses and gave quite different results with the two different stringy varieties. The divergence is so great between the two results that it is thought a different genetic constitution for the two stringy parents affords the most likely explanation. The fact that the same Burpee's Stringless plant was not used involves the possibility that two genetic type of stringless were present rather than two stringy types.

In the preceding material the author has desired especially to indicate the complex inheritance of the character under consideration. There remains the question of the effect that environment may have on the development of the string. Altho no formal data have been collected on this, a number of stringless and stringy varieties have been observed growing in different localities and under varying conditions. No suggestion of a difference in stringiness or stringlessness which could be correlated with the growing conditions has been noted.

Inasmuch as lignification of the string does not start until the pod has developed for about ten days, the age of the pod has some relation to stringiness in the stringy varieties. After lignification starts it appears to gradually increase until the pod matures.

The indications for a complex inheritance of strings may be summarized by observing the variable results secured from different crosses. In certain of these, stringless is dominant and probably the result of a single gene. In other crosses the dominance is reversed, requiring the presence of two factors for a suitable explanation. The two factors have given indications of being complementary. In one cross the two-factor hypothesis postulates that one factor inhibits the action of the other or is epistatic to it. Two types of stringless are shown to exist and probably the same is true for stringy.

INHERITANCE OF FIBER IN THE SIDE WALL OF THE POD

Fiber in the side wall of the pod is a character of distinct economic importance and one that is also very difficult to study genetically. The difficulty arises from the variable expression of the character at different ages of the pod and probably under different growing conditions.

Furthermore, the lignified tissue in this case occurs so that no suitable method of quantitatively measuring it is readily available. A method of making a chemical analysis of the crude fiber of the pod after the string has been removed is now being tried. However, the data so far obtained with it are not sufficient to be included. The data presented here were obtained by examining pods from individual plants and attempting to classify them according to the parental material. The figures are unsatisfactory and are only presented with the hope that they may be of some interest to others working with this character. Two crosses were studied, Longfellow × Wardwell and Pencil Pod × Robust. The Longfellow and Pencil Pod varieties are comparatively free from fiber in the side wall while the others are very fibrous and tough. F_2 results from Pencil Pod × Robust are as follows:

	Fiberless	Fibrous
Observed ratio	34	132
Calculated ratio 3:13	31.1	134.9
Difference	2.9 ± 3.39	
Calculated ratio 1:3	41.5	124.5
Difference	7.5 ± 3.76	

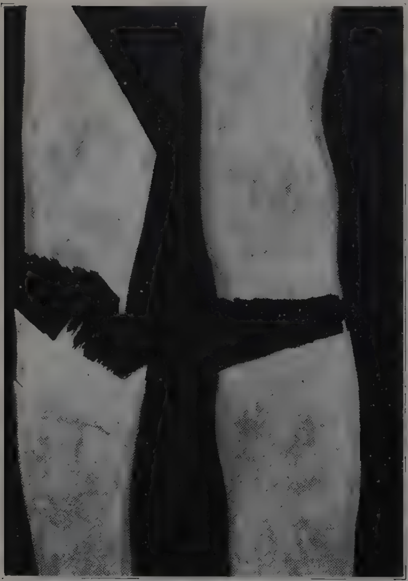

Fig. 6. Fibrous and Fiberless Pods. Enlargement about 2 times

The F_1 of this cross was distinctly fibrous. The F_2 results closely agree with the theoretical 3:13 ratio. They may also be considered to represent a 1:3 proportion. The data secured by growing progenies from some of the F_2 plants are presented in Table V.

Progenies were grown from 4 F_2 plants that were classified as having fiberless pods. Two bred true for "fiberless" but the total number of F_3 plants obtained from both was only 15. One of the 4 lines appeared to be heterozygous giving 3 fiberless to 13 fibrous F_3 plants. The fourth progeny was made up of 7 fibrous-podded plants. Obviously, the number of lines tested was too small to give an accurate test for the genotype of the fiberless F_2 group. If the 34 plants in this group are divided according to F_3 results, the following numbers are obtained: 17 homozygous "fiberless," 8.5 heterozygous, and 8.5 homozygous "fibrous."

TABLE V

F₃ PROGENY OF RANDOM SELECTIONS OF F₂ INDIVIDUALS CLASSIFIED AS FIBERLESS AND FIBROUS, PENCIL POD × ROBUST

Genotype	Designation number	F_2	F_3	
			Fiberless	Fibrous
Homozygous fiberless	80	Fiberless	9	0
	2	do	6	0
Heterozygous	260	do	3	13
Homozygous fibrous	78	do	0	7
Homozygous fiberless	11	Fibrous	12	0
Heterozygous	235	do	10	17
	52	do	6	22
	100	do	4	11
	83	do	4	18
	9	do	3	6
Homozygous fibrous	121	do	0	47
	10	do	0	42
	41	do	0	31
	113	do	0	14
	118	do	0	52
	45	do	0	23
	38	do	0	27
	4	do	0	18
	28	do	0	16
	102	do	0	14
	93	do	0	12
	53	do	0	5
	89	do	0	12
	6	do	0	6

Twenty fibrous-podded F_2 plants produced progenies the following generation. Fourteen gave only fibrous and a total of 323 plants. Five of the lines segregated into the two types, producing a total of 20 fiberless-podded plants to 74 fibrous-podded ones. The theoretical numbers for a single-factor ratio are 23.5 to 70.5, respectively. The difference is 3.5 ± 2.83. If the F_2 is a 3:13 ratio, the heterozygous plants should give progenies showing a 1:3 and a 3:13 ratio in the proportion of 2:4, respectively. Unfortunately, however, the F_3 populations are too small to distinguish the two ratios. The one fibrous-podded F_2 yet to be considered gave a total of 12 fiberless-podded F_3 plants. On the basis of their breeding behavior the 132 fibrous F_2 individuals then may be of the following genotypes: 92.4 homozygous fibrous, 33.0 heterozygous, and 6.6 homozygous fiberless. Combining these figures with those calculated from the fiberless-podded F_2 progenies gives the following:

	Homozygous fiberless	Heterozygous	Homozygous fibrous
F_2 fiberless	17.0	8.5	8.5
F_2 fibrous	6.6	33.0	92.4
Total	23.6	41.5	100.9

Altho the results are not readily explained on a genetic basis, they suggest the difficult and complex nature of the character.

The data secured on the F_2 and F_3 of another cross are entirely different, thereby giving further evidence that the genetics of the character is complex and differs in different varieties. This cross is that made between Wardwell (fibrous) and Longfellow (fiberless). The F_1 was fibrous and the F_2 agrees fairly well with a theoretical one to three ratio. The data for F_2 were 27 fiberless to 68 fibrous, the expected for a 1:3 being 23.75 to 71.25, respectively. The difference is 3.25 ± 2.85.

But here again the F_3 results (Table VI) do not agree with the expected for a single-factor difference. Progenies were grown from 17 fiberless-podded F_2 plants. Ten bred true giving a total of 128 individuals in F3. The progeny from one plant was entirely fibrous-podded and consisted of 6 plants. The remaining 6 were composed of fiberless and fibrous-podded plants. The numbers of each type were 42 fiberless and 58 fibrous; a very poor agreement with the results expected if the character is associated with a single genetic unit.

TABLE VI

F_3 PROGENIES OF RANDOM SELECTIONS OF F_2 INDIVIDUALS CLASSIFIED AS FIBERLESS AND FIBROUS, WARDWELL × LONGFELLOW

Fiberless F_2				Fibrous F_2			
Genotype	Designation number	Distribution in F_3		Genotype	Designation number	Distribution in F_3	
		Fiberless	Fibrous			Fiberless	Fibrous
Homozygous fiberless	1-5	11	0	Homozygous fiberless	3-19	11	0
	3-1	9	0		3-24	20	0
	3-5	13	0		1-6	16	0
	3-8	11	0		1-17	18	0
	3-27	12	0		3-16	20	0
	3-32	11	0		3-18	22	0
	4-5	16	0		4-11	17	0
	4-6	13	0	Heterozygous	3-14	3	18
	4-18	23	0		3-15	3	10
	4-21	9	0		1-13	1	3
Heterozygous	1-2	7	13		3-28	10	4
	1-3	2	3		3-30	6	6
	3-2	6	4		4-2	5	19
	3-9	21	13		4-14	7	1
	3-11	4	16		4-15	6	2
	4-35	2	9		4-16	2	8
Homozygous fibrous	4-24	0	6		3-17	1	13
					4-8	7	21
				Homozygous fibrous	1-8	0	10
					1-22	0	8
					3-7	0	6
					4-25	0	5
					4-26	0	3

Twenty-three fibrous-podded F_2 individuals produced progenies in F_3. Seven of these populations were fiberless, 11 were heterozygous, and 5 had only fibrous-podded plants. The seven with only fiberless had a total of 124 F_3 individuals. The eleven segregating lines had 51 plants without and 105 with fiber. The expected numbers from individuals heterozygous for a single factor are 39 and 117, respectively, the difference between the actual and the theoretical being 12 ± 3.80.

The 5 populations which were entirely fibrous were made up of 32 plants. All are extremely small populations and, therefore, of limited value. It should be noted also that the single plant classified as fiberless in F_2 that gave nothing but fibrous-podded F_3 plants produced a very small population consisting of only 6 individuals.

On the basis of the F_3 figures, it is possible to separate the F_2 phenotypes into the three genotypes considered and to calculate the number in each genotype. The 27 fiberless-podded F_2 and the 68 fibrous should be composed of the following:

	Homozygous fiberless	Heterozygous	Homozygous fibrous
F_2 fiberless	15.9	9.54	1.59
F_2 fibrous	20.7	32.52	14.75
Total	36.6	42.06	16.34

The result is not readily explained without assuming a number of factors that again might not be justified with such small numbers. The above ratio in comparison with a 1:2:1 and a 7:8:1 gives P values that are infinitely small.

Therefore, it is apparent that altho the F_2 ratios give indications of one or two factor differences, the indications are not supported by genotypic tests. Two difficulties which one must consider when studying the inheritance of this character are outstanding. The problem of properly classifying the phenotypes is perhaps the more serious. Altho chemical analysis for crude fiber is a slow and expensive procedure to use for genetic classifications, it may be a means of securing accurate data. The second difficulty is that of securing a large number of seeds from individual plants. This may be overcome to some extent by giving the plants the most favorable growing conditions possible. Also using pole or climbing varieties may be desirable as they are more productive of seed.

INHERITANCE OF WIDTH OF PODS

The varieties which were used for the cross are Wardwell, a wide, flat-podded variety, and Longfellow, a narrow, round-podded type. The difference between the shape of the pods of the two varieties is one of width from suture to suture. This has been demonstrated by measurements of the thickness of the pods on both varieties. No statistically significant difference in thickness was shown. In the F_2 populations so far studied there has not been a significant correlation between pod

TABLE VII

MEANS AND COEFFICIENT OF VARIABILITY FOR POD WIDTHS OF PARENTAL F_1, F_2, AND F_3 GENERATIONS, WARDWELL × LONGFELLOW

Generation	Classes for mean width of pod in centimeters							Total lines	Coefficient of variability classes
	0.9	1.0	1.1	1.2	1.3	1.4	1.5		
P_1		1						1	6
P_1							1	1	9
F_1					1			1	3
F_2				1				1	17
F_3 lines			1					1	0
								0	1
								0	2
								0	3
		2	2		3		1	8	4
	1		2	2	2			7	5
		2	3	1	2			8	6
	1	1	2	2		1		7	7
		2	1	1				4	8
					1			1	9
			1	2	2			5	10
				1				1	11
				2				2	12
			1					1	13
				1	1			2	14

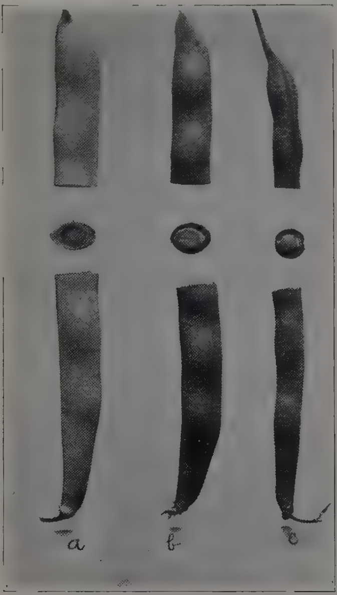

Fig. 7. Representative Pods from Parents a, c, and F_1 b.
Note intermediate shape and width of b.

thickness and the ratio of pod width to pod thickness. The varieties have proved to be distinctly different in width measurements and width has shown a high degree of correlation to the above-mentioned index.

The data obtained are given in Tables VII and VIII. It will be noted that one cross was carried through the F_3 generation and another through the F_2.

The figures were secured by measuring the width of not less than four pods per plant. The average of the four pods was considered to represent the pod width for that particular plant. Plants of the parent varieties were grown in comparison with the F_2 hybrids of both crosses, and with the F_1 of the second cross. The F_1 and F_3 of the first cross were grown without parental material for comparison.

TABLE VIII

Results Secured from the Second Cross of Wardwell × Longfellow

Generation	Year grown	Width classes in centimeters							Mean	Standard deviation	Coefficient of variability
		0.6	0.7	0.8	0.9	1.0	1.1	1.2			
P_1	1928	18	31	3					.671 ± .006	.060 ± .004	9.00 ± .59
P_1	1929		15	36	1				.773 ± .005	.056 ± .004	7.23 ± .48
P_1	1928						9	6	1.140 ± .011	.063 ± .008	5.52 ± .68
P_1	1929						6	15	1.171 ± .008	.053 ± .005	4.52 ± .47
F_1	1928				7	3			.903 ± .012	.055 ± .008	6.10 ± .92
F_2	1929	5	18	39	40	24	1		.850 ± .007	.120 ± .005	14.12 ± .60

In both crosses the F_1 populations were small but appeared to be intermediate for pod width and were no more variable than the parents.

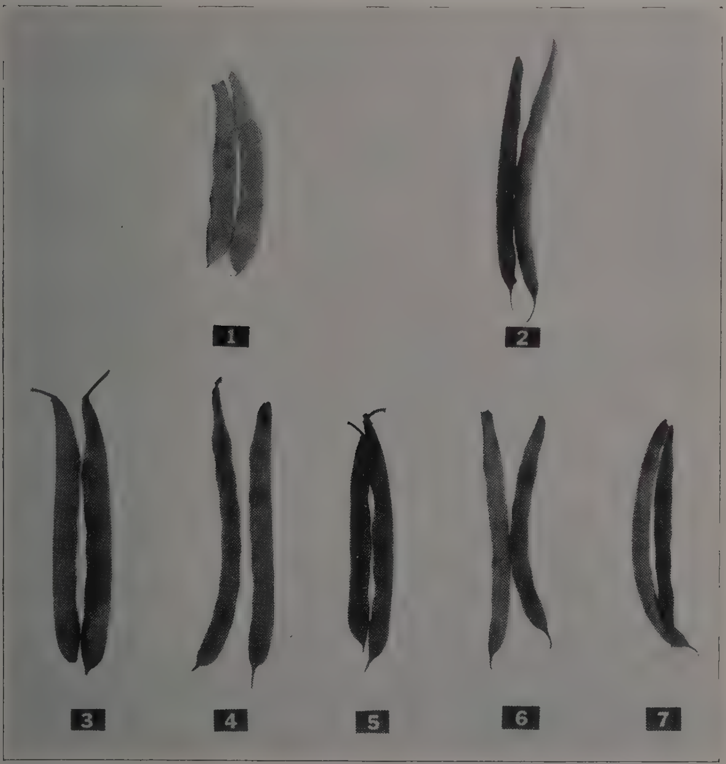

Fig. 8. Representative Pods from Parents 1, 2, and Various F_2 Classes 3 to 7

Altho the F_2 means are intermediate, the variation is quite distinct. The F_3 results are not satisfactory owing to the small populations and to the absence of parental material for comparisons. There is some evidence that certain lines from all the F_2 groups were fairly homozygous in their F3 behavior. This is a possible indication that the character is controlled by a number of factors. Table IX shows a correlation surface for the width of F_2 pods on plants heterozygous for the character and the mean pod width of their F_3 families. These heterozygous plants were selected on the basis of the variability which they showed in F_3. The fact that the correlation is significant is an indication that more than one factor pair is concerned in the development of pod width. If only a single pair were concerned, the probabilities are that all heterozygous F_2 individuals would give approximately the same means in F_3.

The correlation between all F_3 means and their F_2 measurements is given in Table X. The high degree of correlation in this case is believed to indicate an important rôle for inheritance in the development of this character.

TABLE IX

RELATION OF POD WIDTH ON SEGREGATING F_2 PLANTS AND MEAN WIDTH OF THEIR F_3 FAMILIES

Width of segregating F_2 plants	Classes for mean width in F_3, in centimeters								
	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	Total
1.0	2	1							3
1.1			1						1
1.2		1	4						5
1.3			2	2		1			5
1.4					1				1
1.5				1	1				2
1.6								1	1
Total	2	2	7	3	2	1		1	18

$r = .601 \pm .102$

TABLE X

RELATION OF WIDTH OF POD ON F_2 PLANTS AND MEAN WIDTH OF F_3 FAMILIES—WARDWELL × LONGFELLOW

Width of F_2 pods	Classes for mean width in F_3, in centimeters											
	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	Total
1.0	1	1	4	4	1							11
1.1		1	1	2	1							5
1.2	1	1	2	1	6		1	2				14
1.3					3	1	3	1				8
1.4						1	2					3
1.5		1				1		1		1	1	5
1.6									1			1
Total	2	4	7	7	11	3	6	4	1	1	1	47

$r = .66 \pm .056$

LINKAGE RELATIONS

The cross between the Wardwell and Longfellow varieties provided an opportunity to observe the linkage relations for string, for fiber, and for pod width. Altho no definite genetic relationship was indicated between string and the other characters, there is evidence that width of pod is associated with the development of fiber. The F_2 data of the second cross between the above named varieties is given in Table XI. The Wardwell variety is wide and fibrous, whereas Longfellow is narrow and comparatively free of fiber. If the characters tend to remain together, the F_2 plants with fiber should have a greater pod width than those without it. The data show that this actually occurs. The difference between the means is several times greater than its probable error and is, therefore, statistically significant.

Further evidence of this linkage is afforded by a number of varieties of snap beans. No wide-podded variety has been observed that did not develop fibrous tissue in the side walls. Likewise a fibrous round-podded variety is unknown to the writer. Inquiries on this point have been put to several gardeners and scientific workers. In no case has an exception to the above generality been indicated.

One question of interest in this connection is whether both characters are dependent on the same gene or genes or on different ones closely linked in the same chromosome. The F_2 material which was grown in 1929 was arbitrarily separated into narrow and wide pods. Where these were classified for the presence or absence of fiber, all the narrow pods, with but one exception, were noted as being free of fiber. In the case of the wide pods there were only four found to be without fiber. It has already been suggested that fiberless and fibrous pods are often difficult to distinguish accurately. Therefore, these five possible crossover types may have been wrongly classified for fiber. It seems quite probable that the presence of fiber in the side wall of the pods might cause them to develop the flat, wide type rather than the round, fleshy type. A definite answer to this question may result from the F_3 results of the F_2 of 1929. The F_3 records of the previous cross between these varieties were lost before this particular point was checked. If it can be shown definitely that the two characters are controlled by the

TABLE XI

COMPARISON OF THE WIDTHS OF PODS THAT DEVELOP FIBER WITH THOSE THAT DID NOT DEVELOP THIS TISSUE

	Width, centimeters						Mean
	0.7	0.8	0.9	1.0	1.1	1.2	
Fibrous		2.0	15.0	25.0	22.0	1.0	1.004 ± .007
Fiberless	5.0	17.0	22.0	22.0	2.0		0.882 ± .007

same genes, it may be of considerable interest, as it would facilitate the detecting of fibrous pods, and thereby genetic studies of this character.

In concluding the discussion on pod width it can be stated that between the varieties crossed there is undoubtedly a difference of at least two factors. Also pods with fibrous side walls tend to show a greater width than those that are free of such fiber. This may be the result of either a genetic linkage or of multiple allelomorphs.

STUDIES ON POD COLOR

The variety known as Crystal White Wax produces pods of an unusual color. The color is a grayish or silvery one that is readily distinguished from the green and yellow pod colors of the better known varieties. So far as known the inheritance of this color has not been previously investigated.

Tschermak, Emerson, and others have shown yellow to be recessive to green and to differ from it by a single factor. If the silver color of Crystal White Wax also differs by a single factor from green and is not allelomorphic to or linked with the factor for yellow, a cross of silver by yellow would be expected to show a dihybrid segregation. Several crosses involving these various colors have been made. A cross between Wardwell (yellow) and Crystal White Wax (silver) has been carried through the F_3 generation and will be discussed in detail. The F_1 generation from this cross was made up of four green-podded plants. In the F_2 generation, a new color type was segregated as the pure recessive. This is a clear white pod of unusual attractiveness. The two parental colors and green were also recovered in F_2.

According to the description given by Joosten (1927) of the anatomy of the bean pod in cross-section, the color of the green pod is located uniformly in both the inner and outer parenchyma. Altho the yellow type has green plastids when the pods are young, these change to yellow as the pods develop. However, the inner parenchyma of the yellow pod, so far as observed, never appears to contain colored plastids. The silver type has a reduced number of green plastids in the inner parenchyma, and in the outer parenchyma appears to have no color except a narrow band of green adjoining the fibrovascular bundles in this tissue. The white, being a combination of the factors for yellow and silver, is of most interest. It has the colorless inner parenchyma of the yellow type and the colorless outer parenchyma of the silver. The ring of green of the silver adjoining the fibrovascular bundles is present but is greatly reduced in extent.

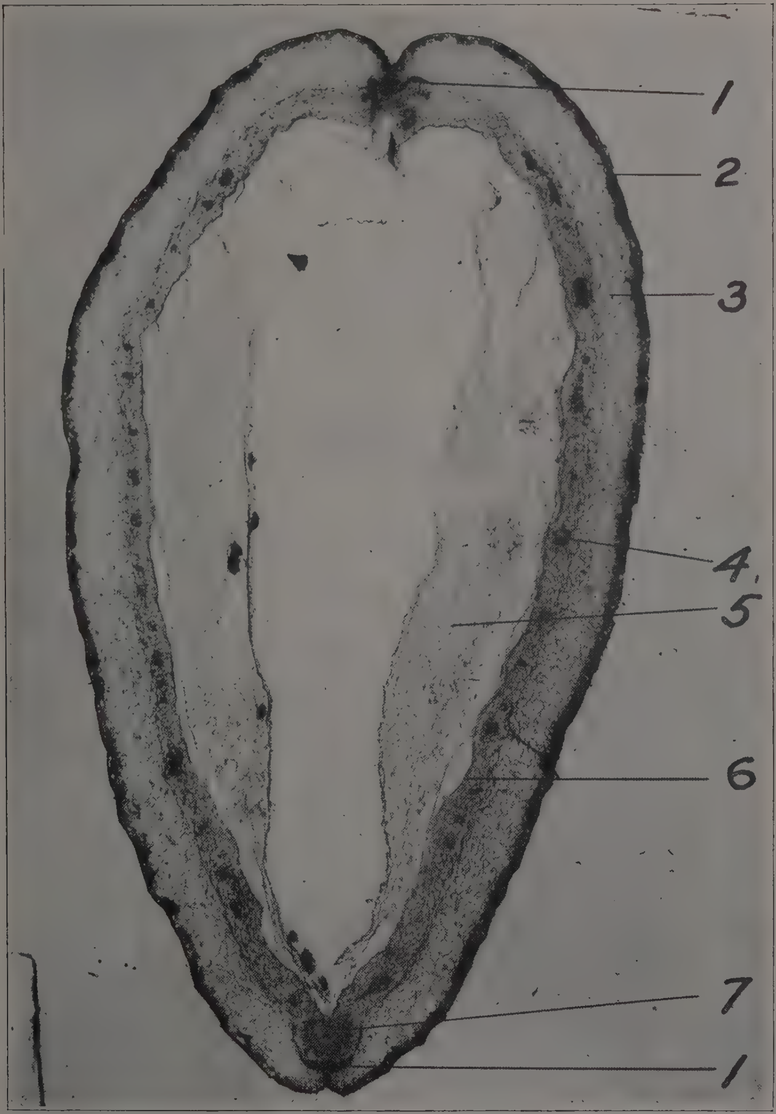

Fig. 9. Transverse Section of a Pod Showing Relative Positions of Different Tissues

Strings, 1; epidermis, 2; outer parenchyma, 3; fibrovascular bundles, 4 and 7; inner parenchyma, 5; fiber of the side wall, 6. Enlargement about 15 times.

The F_2 plants were made up of the following colors:

	Color types			
	Green	Yellow	Silver	White
Observed	96	22	24	8
Calculated 9:3:3:1	84	28	28	9
Difference	12	—6	—4	—1

The P value calculated from the above figures on the basis of a 9:3:3:1 ratio was found to equal .29 or over one chance in four of getting this difference as a result of random sampling.

Thirty of the F_2 green plants were selected at random for testing in F_3. On the basis of the dihybrid hypothesis these green-podded plants would be expected to show four different genotypes as follows:

Number	Genotype	Expected progenies
1	AABB	All green
2	AaBB	3 green, 1 yellow
2	AABb	3 green, 1 silver
4	AaBb	9 green, 3 yellow, 3 silver, 1 white

Three of the total of 30 plants bred true for green pods; 5 segregated for green and yellow, 9 for green and silver, and 13 for green, yellow, silver, and white. Comparison of the observed with the calculated follows:

	Color types			
	Green	Yellow	Silver	White
Observed	3.0	5.0	9.0	13.0
Calculated 1:2:2:4	3.3	6.7	6.7	13.3
Difference	—0.3	—1.7	2.3	—0 3

The P value for these figures is 0.74.

The 13 plants segregating for 4 colors would be expected to give a ratio of 9:3:3:1 or a duplicate of the F_2 results. The observed and expected results from the 13 plants follow. The P value was calculated from these data to be .62.

	Color types			
	Green	Yellow	Silver	White
Observed	288	94	82	30
Calculated 9:3:3:1	277	93	93	31
Difference	11	1	—11	—1

Five F_2 green-podded plants gave only green and yellow in F_3. The total number of F_3 individuals was 160, of which 117 were green an 43 were yellow; the expected numbers are 120 and 40, respectively. The deviation therefore is 3 ± 3.69.

Nine F_2 green-podded plants produced only green- and silver-podded individuals in F_3, the total number being 361. Of these, 275 were green- and 86, silver-podded; the expected numbers are 271 and 90, respectively. The deviation is 4 ± 5.55.

Progenies from 10 F_2 yellow-podded plants selected at random were grown in F_3. These F_2 plants were expected to show 2 genotypes in the proportion of one homozygous for yellow to 2 heterozygous for yellow and white. Seven of the 10 plants produced both yellow- and white-podded individuals in F_3, while 2 produced only yellow-podded ones, and one produced green- and yellow-podded individuals. Very probably this individual bore green pods and was wrongly classified in the F_2 records. When a green-podded plant reaches maturity, the chlorophyll gradually disappears from the pods at which time such a plant may readily be mistaken for a yellow-podded one. The F_3 results are approximately those which would be expected from a plant heterozygous for green and yellow. Disregarding this line, the 9 yellow-podded F_2 plants give a deviation from the theoretical genotypic ratio of 1 ± 0.95.

The F_2 yellow-podded plants producing both yellow and white pods in F_3 gave a total of 181 individuals. Of these 137 were yellow and 44 were white; the expected numbers were 136 and 45, respectively. The deviation is equal to 1 ± 3.93. The two plants that gave only yellow-podded individuals produced a total of 129 F_3 plants. The one individual which gave green and yellow produced 10 green to 4 yellow. This is a close approximation to the ratio expected from a green plant heterozygous for green and yellow.

Progenies also were grown from 10 of the F_2 silver-podded plants. They would be expected to show the same type of behavior as the F_2 yellow-podded individuals. Six of the 10 gave silver and white, and 4 gave only silver; the expected numbers are approximately 7 and 3, respectively. The deviation is 1 ± 1.0. The total number of plants obtained in the F_3 generation from the segregating F_2 individuals was 151, of which 107 were silver and 44 white. The theoretical numbers are 113 and 38, making the deviation equal to 6 ± 3.59.

Six progenies were grown from plants that bore white-colored pods in F_2. The total number of F_3 individuals grown was 136, all of which bore only white-colored pods.

Two additional crosses between yellow- and silver-podded plants were carried through the F_2 generation. A cross of Refugee Wax by Crystal White Wax yielded 2 green-podded F_1 plants. The F_2 of this cross gave the following:

	Color types			
	Green	Yellow	Silver	White
Observed	55.0	13.0	14.0	4.0
Calculated 9:3:3:1	48.6	16.2	16.2	5.4
Difference	6.4	—3.2	—2.2	—1.4

The P value for these figures is 0.56.

From the second cross, which is the reciprocal of the above, 3 green-podded F_1 plants and the following F_2 numbers were obtained:

	Color types			
	Green	Yellow	Silver	White
Observed	114.0	32.0	22.0	14.0
Calculated 9:3:3:1	102.4	34.1	34.1	11.4
Difference	11.6	—2.1	—12.1	2.6

The P value in this case is 0.11.

The white-podded segregate crossed with silver or yellow would be expected to show a single-factor behavior. When it was crossed with yellow, one yellow-podded F_1 plant was obtained. In the next generation, 38 yellow-podded plants and 9 white-podded ones were produced. The calculated numbers are 35.25 and 11.75, respectively. The difference is 2.75 ± 2.0. White by silver gave one silver-podded F_1 plant. In F_2, 12 plants were silver-podded and 3 were white-podded. The calculated numbers for these figures are 11.25 and 3.75, respectively. The difference is 0.75 ± 1.13.

The single-factor difference between silver and green is shown by a cross of Michigan Robust (green-podded) × Crystal White Wax (silver-podded). The F_1 from this cross consisted of 3 green-podded plants . In F_2 there were 60 plants with green pods and 24 with silver pods. The expected numbers for a three to one ratio are 63 and 21, respectively. The deviation is, therefore, 3 ± 2.68. In the F_3 generation progenies were grown from 10 plants that bore green pods in F_2. Three of the progenies consisted of only green-podded plants and 7 were made up of green- and silver-podded ones. The expected numbers are 3.3 and 6.6, respectively. The deviation is .3 ± 1.0. The 7 heterozygous lines gave a total of 56 plants of which 47 were green-podded. The calculated ratio is 42 and 14, making the deviation 5 ± 2.19. Progenies were also grown from 4 silver-podded F_2 plants. A total of 32 plants were produced, all having silver-colored pods.

SUMMARY AND CONCLUSIONS

Data of three generations from three crosses on the mode of inheritance of stringlessness are presented. Data from two of the crosses can be explained by assuming a single-factor difference between the varieties crossed. F_2 and F_3 results from a third cross can be explained by assuming a two-factor relationship. One dominant factor produced stringlessness but may be inhibited in its action by a second factor. F_2 results from a number of additional crosses indicate the existence of two genetic types of stringless and possibly two types of stringy among the varieties used for the crosses.

Two crosses were studied for three generations to determine the nature of the inheritance of fiber in the side wall of the pod. Owing to difficulties of making classes for this character and to the limited amount of data obtained on it, no definite statement can be made regarding its inheritance.

A cross between the varieties Wardwell and Longfellow indicates that pod width is inherited as a quantitative character and therefore may be associated with a series of multiple factors. The cross was carried through the F_3 generation in one case and through the F_2 in another instance. It is hoped the data at hand may be clarified by growing a number of F_3 populations from the latter cross.

Width of pod is associated with fiber of the side wall of the pod, and the two characters may depend on the same factor or factors.

The inheritance of the pod color of the variety Crystal White Wax was found to give monohybrid results when crossed with green. A limited amount of data on the F_1, F_2, and F_3 of this type of cross was secured. When Crystal White Wax was crossed with a yellow-podded variety the F_2 and F_3 generations gave results which agree with the theoretical numbers for a dihybrid behavior. The double recessive from this cross represents a new pod color so far as known by the author. When crossed with either yellow- or silver-podded plants, the F_2 numbers are approximately in the ratio of three yellow or silver to one double recessive. The color regions for the four types of pods are described with reference to the anatomical structure of the pod.

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A Study of Senescence in the Red Raspberry Cane

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CONTENTS

Page

Introduction 5

Review of literature 5

Definition of terms used in relation to the cane and its parts 7

Increase in diameter of old canes 8

Internal anatomy 13

- Materials and methods 13
- Resting cambium 14
- Response of cambium to the stimulus from developing buds 14
- Development of new xylem in the old cane 19
- Development of new phloem in the old cane 26
- Decline of the phloem 28

Behavior of stem cuttings 30

Conclusions 33

Summary 33

Literature cited 35

ILLUSTRATIONS

Page

Fig. 1. Old cane showing obvious increase in diameter just below vigorous laterals 9

2. Diameters at successive heights in young and old canes 11

3. Cross-section from the base of a Ranere cane in March showing resting cambium 14

4. Cross-section from the base of a Cuthbert cane in March showing resting cambium 15

5. Feeble activity of the cambium just below a vigorous young lateral from the central region of a Cuthbert cane 16

6. Cambium just below a well-developed lateral with blossom buds appearing 16

7. Cambium from the central region of a Cuthbert cane, 5 cm. below a vigorous lateral with first blossoms open 17

8. Cambium at the base of a Cuthbert cane showing feeble activity similar to that shown in Fig. 7 17

9. Irregular margin of the xylem at the base of Cuthbert cane 18

10. Base of an Evergreen blackberry cane at the end of the second year .. 19

11. Longitudinal section made in December through the base of a lateral on a vigorous old cane of the Latham variety 20

12. Cross-section through the base of a vigorous lateral from the same cane as Fig. 11 21

13. Section cut .5 cm. below Fig. 12 22

14. Section cut 1 cm. below Fig. 12 22

15. Section cut 1.5 cm. below Fig. 12 23

16. Section cut 2 cm. below Fig. 12 23

17. Cross-section made just below a lateral of medium vigor in the tip region of a Cuthbert cane 24

18. Complete ring of new xylem (X) in central region of Latham cane with many vigorous laterals 24

19. Complete ring of new xylem (X) at the base of a Latham cane 25

20. Cross-section of tip region of Cuthbert cane 27

21. Cross-section from the base of a Ranere cane cut in January after the fruiting season 29

22. Base of a hardwood cutting made in January, 1930, from a young cane of Latham 31

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A summary of this report appeared under the title, "Cambial Activity in the Red Raspberry Cane in the Second Season" in the American Society for Horticultural Science Proceedings 26:278-80. 1929.

A STUDY OF SENESCENCE IN THE RED RASPBERRY CANE[1]

W. G. Brierley

INTRODUCTION

Many descriptions of the growth habit of the red raspberry plant *Rubus strigosus* appear in horticultural literature. Bailey (1) describes the raspberry as a plant with a perennial root and erect, or nearly erect, biennial canes. Under *Rubus* he says that in raspberries and blackberries the canes bear the second year and then die or become very weak. Darrow (4), Hedrick (11), and others, present similar descriptions. But in none of these is there any attempt to explain this behavior. Altho these writers do not discuss certain phases of the growth habit in detail, it is obvious that the apical meristem of the cane ceases to function at the end of the first year and that there are no winter buds formed on the cane in the second season. The development of the young cane, its behavior in the fruiting season, and subsequent decline and death are of necessity given consideration in numerous publications dealing with the practice of pruning. Apparently no attention has been given in these pruning studies either to radial growth or to the internal structure of the fruiting cane. As the structure and growth of the cane appear to have a relation to the fruiting performance and to pruning practices, the present studies were undertaken to determine the nature and extent of cambial activity and radial growth in the cane in the second year.

REVIEW OF LITERATURE

Apparently, there have been no reports upon the behavior of the cambium in the red raspberry in the second season, but studies of cambial activity and radial growth in other plants have a bearing on the subject. Hartig (9), writing in 1878, appears to have been the first to report upon the time of cambial activity in woody stems. From his studies, he concluded that in larch and maple cambial activity occurred first in the youngest twigs and then gradually extended downward, but that this behavior was not typical of some other trees. Gulbe (8) found that cambial activity in many species began with bud development, but that in some species this activity was delayed until the leaves were completely developed. Strassburger (29) stated that in general cambial activity begins in one-year shoots just back of unfolding buds and proceeds downward to the larger branches and trunks on which it usually begins uniformly and at about the same time from top to bottom. Jost (12) presented further evidence of this relation between bud development and cambial activity. Jost (13) later described the xylem development as a wedge-shaped strip of new wood, which gradually became thinner and finally disappeared in the direction of the stem base. This wood strip was largest below the strongest shoots, and in twigs with poorly developed shoots, very limited areas of new wood were formed. Mer (20) noted that cambial activity appeared first in the youngest twigs, but in certain cases was evident on one side of the twig and not on another. Reiche (23) showed that radial growth of trees did not occur unless bud development preceded it. Lutz (17) also indicated that the initiation of new growth is from above downward, but showed further that branches of young trees of certain species disbudded in March remained healthy but with no radial growth. Hastings (10) found the first new wood was formed in the neighborhood of terminal buds and was not continuous around the stem. Simon (25) concluded from similar studies that in certain woody species secondary thickening spread downward very slowly. Pfeffer (21) found that the secondary growth of xylem in trees began and ended sooner than that of the phloem. Knudson (15), however, found that in the American larch new phloem was formed before new xylem appeared, but the greatest growth of phloem coincided with the greatest development of xylem. Grossenbacher (7) in 1915 presented an excellent review of the literature relating to radial growth, in which he showed that in general cambial activity begins in young shoots just back of unfolding buds and proceeds downward to the older parts of the plant.

---

[1] Also submitted to the faculty of the Michigan State College of Agriculture and Applied Science in partial fulfillment of the requirements for the degree of Doctor of Philosophy, granted June, 1930.

Few reports relating to cambial activity of fruit plants appear in the literature. Knudson (16) found that in the grape new phloem and xylem were formed simultaneously, the cambium becoming active when the leaves were almost completely developed. In the apple, this activity was found to be similar to that of the grape in that it was preceded by considerable leaf development. In the peach, cambial activity was found to begin with the opening of the buds. Knight (14) showed that in the apple cambial activity was very similar to that of other woody plants, in that new xylem was formed first in the region bearing developing buds, and that wherever bud-growth occurred new xylem formation invariably accompanied it. This activity proceeded downward into "bare" regions of the stem in which buds had not developed. Swarbrick (27) also found that in the apple, xylem differentiation began in the terminal region of shoots and spurs and progressed downward towards the roots. He observed that at the base of one-year-old shoots the first xylem differentiation was down the sides of the "vascular bundles," and that the vigorous development of a spur on a short lateral branch resulted in early xylem formation in the branch on the side corresponding to the point of spur insertion. Swarbrick (28) later showed that there was no cambial activity in areas on an apple shoot, which were isolated by a double girdle and disbudded. When buds remained and developed, xylem formation was found to be proportionate to the vigor of the shoot. In disbudded isolated areas, the cambium lost its meristematic condition by September and xylem was not formed at any time. Sledge (26) found that in hardwood cuttings of the apple and other species cambial activity not only spread downward from the tips due to the stimulus from developing shoots, but also spread upward from the proximal ends. He attributed this latter type of cambial activity to a stimulus from the wound at the base of the cutting.

As previously stated nothing appears in the literature in relation to cambial activity in the raspberry. However, in some studies of the behavior of the European blackberry, Bonnier (3) found that some canes could be kept alive into the third and fourth seasons, by trellising them in a vertical position. Altho he noted a marked decline in vigor of growth he found that a ring of new wood and phloem was formed in some of these canes in the third season, but this ring was much narrower than the rings formed in the first and second years. MacDaniels (18), in his studies of fruit bud formation in the genus *Rubus,* found that when old canes of the Herbert raspberry were disbudded they generally died, but disbudded old canes of the Snyder blackberry generally lived and frequently produced fruiting laterals In the present studies some old canes of the Latham variety which were disbudded in early spring died and dried up by midsummer. This behavior of the raspberry is in marked contrast to that of the woody species studied by Lutz (17). Bennett (2) attempted to transmit virus diseases in the raspberry by budding and bark grafting, but found it extremely difficult to obtain successful unions. The present studies show that the cambial activity of the red raspberry cane in the second season is much the same as that of other woody stems, but that this activity in general is feeble.

DEFINITION OF TERMS USED IN RELATION TO THE CANE AND ITS PARTS

In descriptions of the raspberry plant, or of its horticultural varieties, or in discussions of pruning there is some confusion in regard to the names given to the various parts of the cane. In order to avoid this confusion, the following definitions are offered, covering the terms used in these studies:

Young cane.—The new growth usually arising as suckers from the root, or from the underground portion at the base of an old cane. In some localities these new canes are called "turions." With regard to season, the young cane is considered to continue through the winter until the end of the dormant season. On the young cane, winter buds are developed from which lateral shoots arise in the second year.

Old cane.—The cane from the beginning of growth in the second year until the end of that season, when the cane usually dies. Growth of the old cane results chiefly in the production of leafy lateral shoots on which the flowers and fruits are borne. Under normal conditions no terminal growth occurs in the second year and no winter buds are developed either on the cane or laterals.

Branch.—A division of the young cane, developed in the first year. Essentially the same as a young cane, but arising from it instead of from the crown or root.

Lateral.—A leafy shoot of the old cane or branches developing from a winter bud and usually bearing flowers and fruits. Many of the laterals may produce neither flowers nor fruits. To distinguish between them on the basis of performance they may be called fruiting laterals or barren laterals.

INCREASE IN DIAMETER OF OLD CANES

Observations of old canes of the red raspberry do not as a rule reveal any material increase in diameter in the second season. In some cases, as shown in Figure 1, an increase in cane diameter is readily discernible below vigorous laterals. Bonnier (3) found narrow "annual rings" formed in the second and third seasons in specially handled blackberry canes, but nothing has been found in the literature to show that raspberry canes behave in this way. To obtain some detailed evidence on this phase of the problem, measurements were made of dormant young canes and of old canes at the end of the second season. Beginning 1 cm. above the ground, measurements were made with a vernier caliper at 5 cm. intervals up to the tips of each cane. The average of two measurements taken at approximately right angles to each other was used as the diameter at each height. The canes were arbitrarily placed in three classes with regard to diameters at the base as follows:

(1) Vigorous canes, above 1.25 cm.; (2) medium canes, from 1.00 to 1.25 cm.; (3) weak canes, less than 1.00 cm. The average diameters for the dormant young canes are given in Table I. The measurements of the available old canes are given in Table II. The data from these tables are shown graphically in Figure 2.

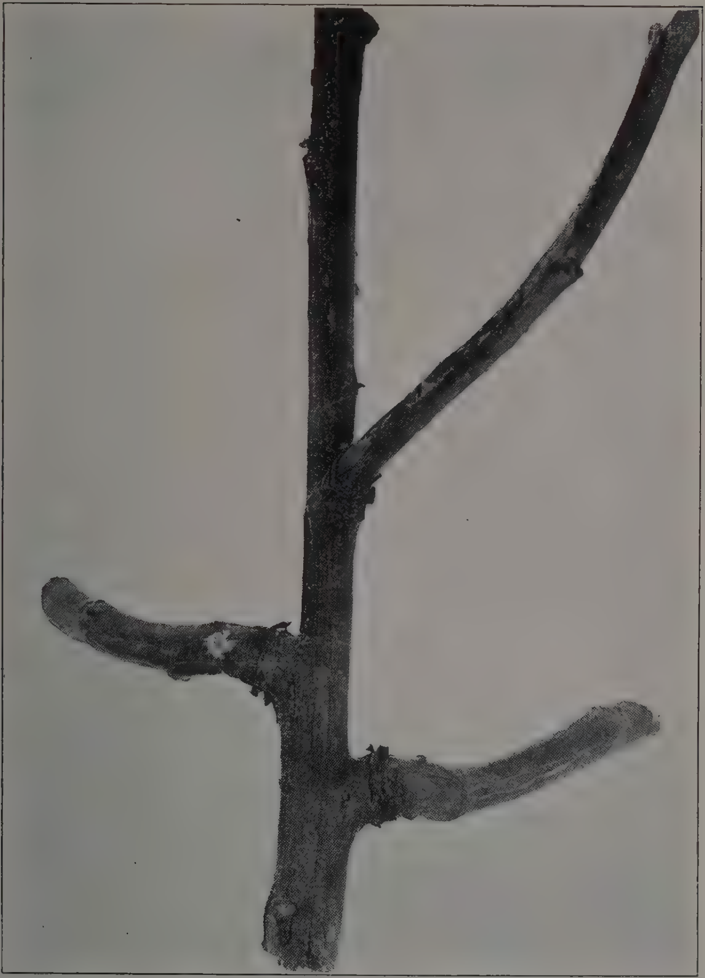

Fig. 1. Old Cane Showing Obvious Increase in Diameter Just Below Vigorous Laterals

Altho the number of canes in each class was not large and no old canes were available with a diameter of more than 1.25 cm. at the base, the data indicate that the red raspberry cane generally does increase in diameter in the second season. The diameters of the dormant young canes decline very regularly from the base upward, regardless of cane vigor. The old canes show a slight increase in diameter for a distance of about 25 cm. from the base. Beyond that point the diameters decline more or less regularly with increasing height. Measurements of the old canes at hand could not be made up to the same height as the new canes because of tip pruning. Comparisons between the

TABLE I

DIAMETERS OF NEW CANES AT SUCCESSIVE HEIGHTS

Height above ground in cm.	Vigorous		Medium		Weak	
	No. canes	Average diameter in cm.	No. canes	Average diameter in cm.	No. canes	Average diameter in cm.
1	15	1.42	18	1.12	18	0.89
6	15	1.38	18	1.05	18	.85
11	15	1.34	18	1.02	18	.81
16	15	1.30	18	.99	18	.79
21	15	1.27	18	.97	18	.77
26	15	1.25	18	.96	18	.75
31	15	1.23	18	.93	18	.72
36	15	1.20	18	.91	18	.70
41	15	1.17	18	.89	18	.68
46	15	1.15	18	.87	18	.66
51	15	1.12	18	.85	18	.64
56	15	1.09	18	.83	18	.61
61	15	1.08	18	.80	18	.58
66	15	1.05	18	.78	18	.57
71	15	1.03	18	.75	16	.56
76	15	1.01	18	.73	16	.54
81	15	.98	18	.70	16	.52
86	15	.95	18	.68	15	.51
91	15	.91	18	.65	14	.50
96	15	.90	18	.64	13	.48
101	15	.86	18	.62	10	.48
106	15	.83	17	.61	10	.44
111	15	.80	17	.58	10	.41
116	15	.77	17	.55	10	.39
121	15	.74	16	.51	10	.37
126	15	.72	15	.49	8	.36
131	15	.68	13	.47	6	.33
136	15	.64	12	.45	—	—
141	12	.64	10	.44		
146	12	.59	10	.40		
151	10	.61	9	.39		
156	10	.57	6	.41		
161	10	.53	5	.39		
166	9	.51	4	.37		
171	9	.49	—	—		
176	9	.47				
181	8	.45				
186	7	.42				
191	6	.41				
196	6	.39				

old and young canes of the same relative vigor show that the old cane has a small but constant advantage in diameters except at the base. This relation is shown clearly in Figure 2. These data indicate that, in the average old cane, radial growth occurs in the central and upper portions but not at the base close to the ground.

Further evidence of the failure of the old cane to increase in diameter at the base was obtained by examining the tissues exposed in cross-section when canes of this age were cut off at the ground. Old canes of Cuthbert and Latham from several sources were examined in this manner, by means of a hand lens of suitable magnifying power. In doubtful cases a free-hand section was cut from the base of the

TABLE II

DIAMETERS OF OLD CANES AT SUCCESSIVE HEIGHTS

Height above ground in cm.	Vigorous		Medium		Weak	
	No. canes	Average diameter in cm.	No. canes	Average diameter in cm.	No. canes	Average diameter in cm.
1	*	*	25	1.08	30	0.85
6			25	1.09	30	.86
11			25	1.10	30	.87
16			25	1.09	30	.87
21			25	1.09	30	.87
26			25	1.08	30	.85
31			25	1.07	30	.84
36			25	1.04	30	.83
41			25	1.01	30	.81
46			25	.99	30	.80
51			25	.96	30	.78
56			25	.95	30	.76
61			25	.92	29	.74
66			25	.91	28	.74
71			25	.87	28	.71
76			25	.84	26	.68
81			25	.80	21	.67
86			23	.77	17	.66
91			21	.74	12	.67
96			17	.72	10	.66
101			10	.69	6	.65
106			6	.74	6	.61
111			4	.72	—	—
116			3	.65		

* None available.

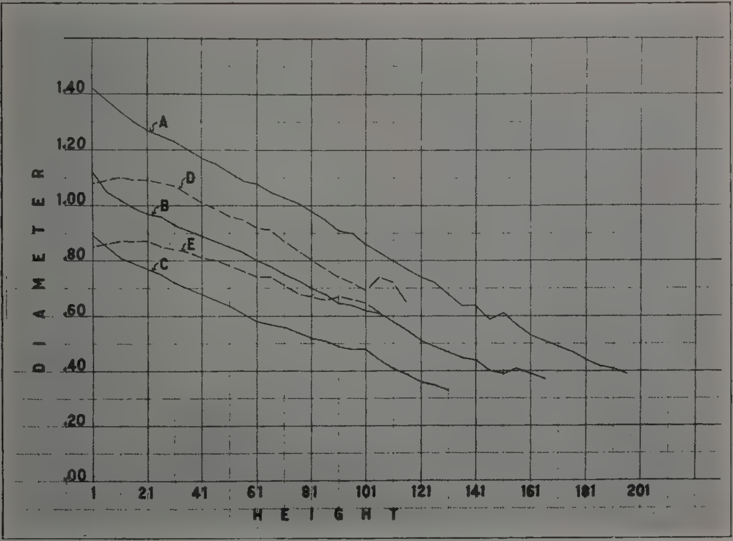

Fig. 2. Diameters at Successive Heights in Young and Old Canes

A. Vigorous young canes; diameter at base greater than 1.25 cm.
B. Young canes of medium vigor; diameter at base from 1.0 to 1.25 cm.
C. Weak young canes; diameter at base less than 1.0 cm.
D. Old canes of medium vigor; similar to B.
E. Weak old canes; similar to C.

cane and examined under a binocular microscope. For convenience in tabulating the data, all canes less than 1 cm. in diameter at the base were classed as weak and all of greater diameter classed as vigorous. These data are shown in Table III.

TABLE III

Occurrence of New Xylem at the Base of Old Canes

Variety and source	Vigorous canes (More than 1 cm. in diameter at base)				Weak canes (Less than 1 cm. in diameter at base)			
	Present	Per cent	Absent	Per cent	Present	Per cent	Absent	Per cent
Cuthbert, Mich.	18		56		15		77	
Cuthbert, Mich.	0		93		1		63	
Cuthbert, Wash.	1		21		0		30	
Total	19	10.0	170	90.0	16	8.6	170	91.4
Latham, Mich.	11		11		7		92	
Latham, Minn.	4		30		0		82	
Latham, Minn.	8		33		2		11	
Total	23	23.7	74	76.3	9	4.6	185	95.4
Total	42	14.7	244	85.3	25	6.6	355	93.4
Total, all canes both varieties	67	10.1	599	89.9				

Table III indicates that in slightly more than 10 per cent of the old canes examined new xylem was found at the base ranging in amount from a few scattered vessels and fibers up to well developed complete rings. New xylem was found more frequently in vigorous canes (14.7 per cent) than in weak canes (6.6 per cent). Very little difference was found between vigorous and weak canes in the Cuthbert variety, but vigorous canes of the Latham showed new xylem occurring much more frequently (23.7 per cent) than weak canes (4.6 per cent). The difference between the two varieties is thought to be due to the greater tendency of Latham canes to develop vigorous laterals near the base. In some unpublished studies of the effect of various pruning heights upon cane behavior in the Latham, the writer has found that basal laterals originating within 1 to 5 cm. from the ground quite frequently grow to a length of 100 cm. or more. Occasionally these laterals are barren and develop into new canes ranging from 150 to 200 cm. in height. In cases of this kind a well-developed complete ring of new xylem has been found at the base. This type of growth has been observed in the Cuthbert, but does not appear to be as common.

As only one out of 10 old canes apparently has new xylem at the base, and as little or no new phloem is formed close to the ground in the average cane (as will be shown later), it is obvious that the majority of old canes depend almost entirely upon old tissues for the conduction of water and foods through the basal region. It is considered possible that this condition at the base may in part explain the fact that old canes generally are less vigorous than young canes.

INTERNAL ANATOMY

Materials and Methods

In these studies, sections were cut from both young and old canes in the fresh condition, without killing or embedding the material. The sections were cut about 20 to 30μ in thickness, with a slide microtome. The canes were found to be firm enough to handle in this manner if, when the microtome clamp was adjusted, care was exercised not to crush the shell of wood surrounding the extensive area of pith. The staining of this material was found to be most satisfactory when a one per cent aqueous solution of safranin was used in combination with Delafield's hematoxylin. These stains usually produced the most satisfactory results when somewhat diluted. Better results also were obtained when the hematoxylin was used before the safranin. The usual procedure was followed with regard to dehydrating in alcohol and clearing in xylol. Neutral Canada balsam was used for mounting the material. At times it was found difficult to hold the safranin stain in the xylem. Apparently the xylem region was sufficiently acid in reaction to cause the bleaching of the stain soon after mounting. This difficulty was avoided to a considerable extent by using in one stage of the dehydration process 95 per cent alcohol to which a few drops of a dilute solution of sodium hydroxide were added.

Most of the cane material for these studies was obtained from the Latham and Cuthbert varieties from various sources in Michigan and Minnesota. Some use was made of canes of the Ranere (St. Regis) variety obtained from Ohio, Illinois, and Washington, D.C. For purposes of comparison, some canes of the Cuthbert raspberry and the Evergreen and Logan blackberries were obtained from western Washington.

In a majority of cases, when canes were examined, sections were made from four general regions of the cane. The first sections were cut as close as possible to the base; others were then cut from a point 5 to 10 cm. higher up on the cane, from the central region of the cane, and from the tip region. Transverse, radial, and tangential sections were made at each point. It was found during the progress of the work that the evidence relating to radial growth was shown most clearly in the transverse sections, so this form was emphasized in the later work. Transverse sections were made from some old canes at 5 or 10 cm. intervals from the base to the tips, to ascertain the location and extent of development of new xylem.

In the process of sectioning, the pith was found to crush or tear away if the sections were cut sufficiently thin to be of value. Also the loose outer layers of the periderm usually were torn off. However, the loss of these portions of the sections was not serious as the studies deal mainly with the cambium and adjacent tissues.

Resting Cambium

From studies of the dormant young cane and of old canes at the beginning of the growing season, it appears that the cambium is in the resting condition noted by Roberts (24) in some apple seedlings. Figures 3 and 4 illustrate this condition in the dormant young canes of Ranere and Cuthbert.

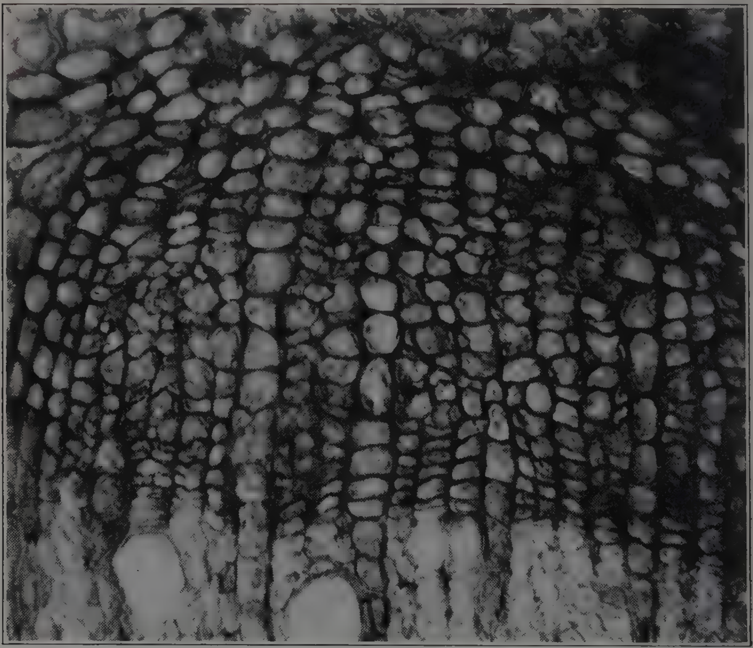

Fig. 3. Cross-section from the Base of a Rȧnere Cane in March Showing Resting Cambium. ×435

Response of Cambium to the Stimulus from Developing Buds

The cambium in the old cane seems to respond very slowly and feebly to the stimulus from developing shoots. Examinations of old canes from plants grown in the greenhouse indicate that the cambium in the cane generally did not become active until the laterals were well developed. In vigorous canes, particularly from plants fertilized with a moderate application of sodium nitrate just before the buds opened, some cambial activity was found when the laterals, with several partially unfolded leaves, were not over 5 cm. in length. This activity, as evidenced by the formation of new xylem, was feeble and occurred only immediately below the most vigorous laterals. Figure 5 shows this condition in the central region of a Cuthbert cane. In other canes, particularly those making a weak growth in the second season, cambial activity was not apparent even when the laterals were 20 cm. in length, with several well-developed leaves and with the blossom buds appearing. Figure 6 illustrates this condition in the tip region of a Cuthbert cane.

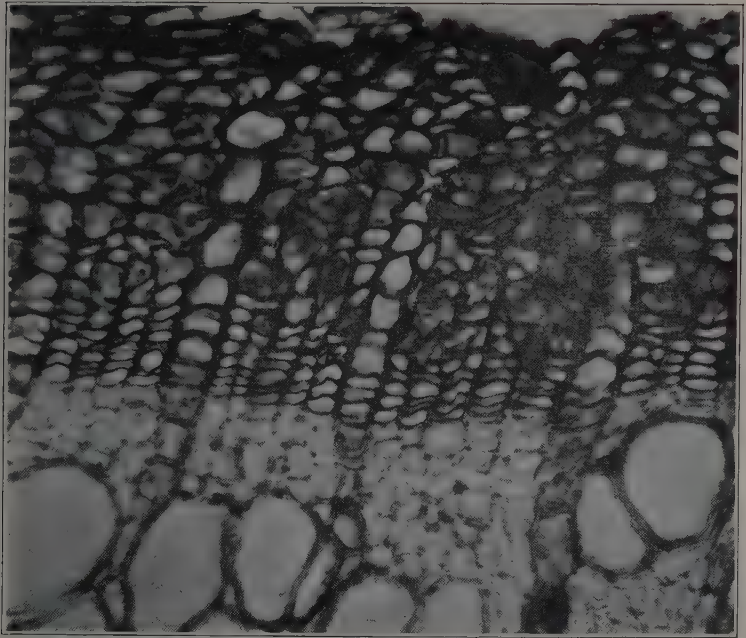

Fig. 4. Cross-section from the Base of a Cuthbert Cane in March Showing Resting Cambium. ×435

The development of cambial activity in response to the stimulus from growing laterals appears to proceed down the cane very slowly and is markedly feeble at a point only a few centimeters below a lateral. Even in vigorous canes the activity of the cambium a short distance below a lateral appeared to be restricted in many cases to an increase in the radial diameters of the cambial cells. The cambium at these points, also, seems to have failed to maintain its width, indicating that some of the outer cells had differentiated into phloem elements, but that no new cambial cells were formed. This condition is shown in Figure 7.

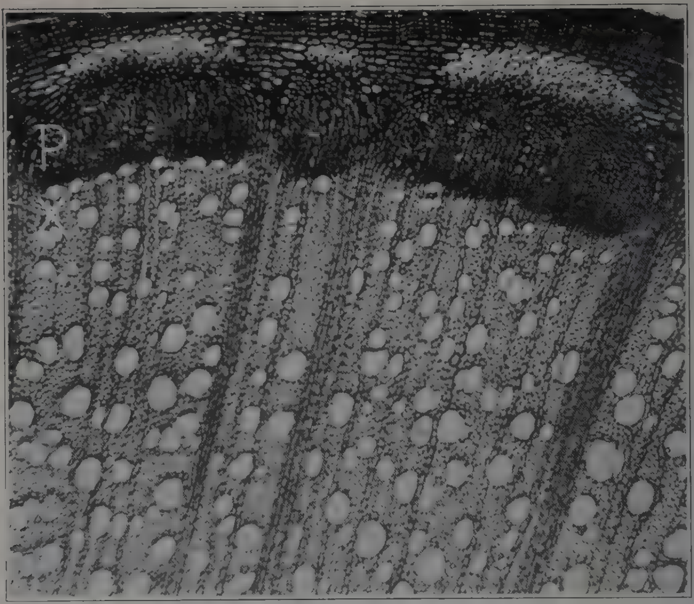

Fig. 5. Feeble Activity of the Cambium Just Below a Vigorous Young Lateral from the Central Region of a Cuthbert Cane

New xylem (X) very limited in amount. Darker staining of the inner phloem (P) indicates that these cells are of recent development. ×96.

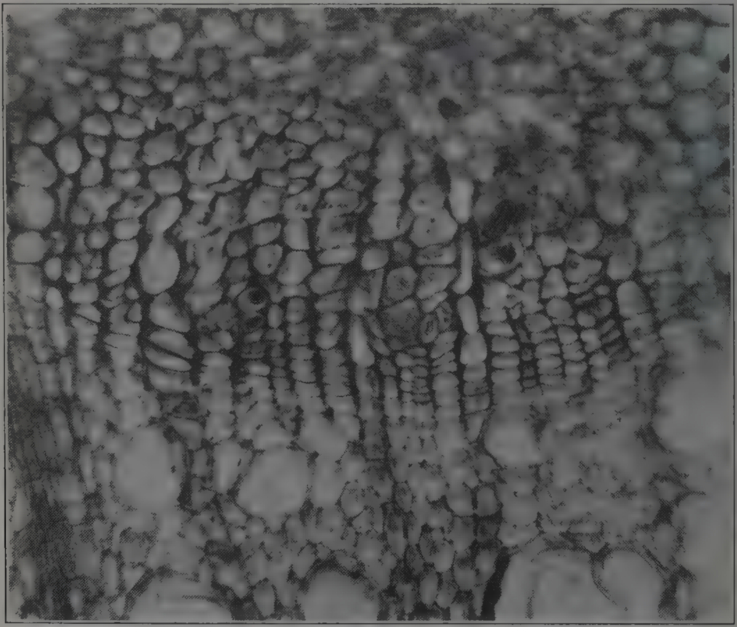

Fig. 6. Cambium Just Below a Well-developed Lateral with Blossom Buds Appearing From the tip region of a weak Cuthbert cane. No activity apparent. ×435.

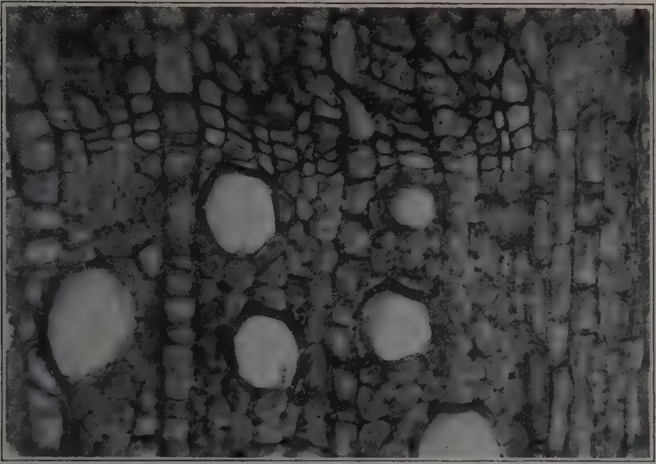

Fig. 7. Cambium from the Central Region of a Cuthbert Cane, 5 cm. Below a Vigorous Lateral with First Blossoms Open

Feeble activity evidenced by reduction in width of cambium and an increase in radial diameter of the cells. ×435.

Altho in the majority of old canes the cambium in the basal region appears to remain in the resting condition when no laterals develop in that region, a feeble development similar to that noted above was found in some canes which did not develop vigorous laterals near the ground.

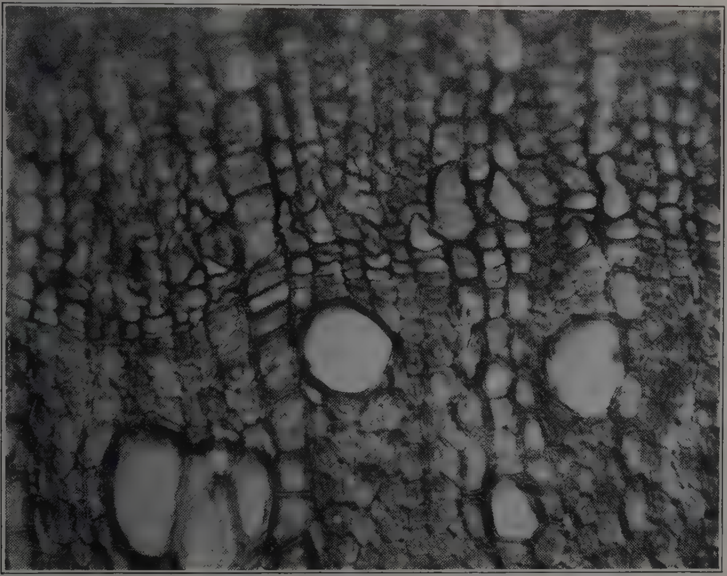

Fig. 8. Cambium at the Base of a Cuthbert Cane Showing Feeble Activity Similar to That Shown in Figure 7. ×435

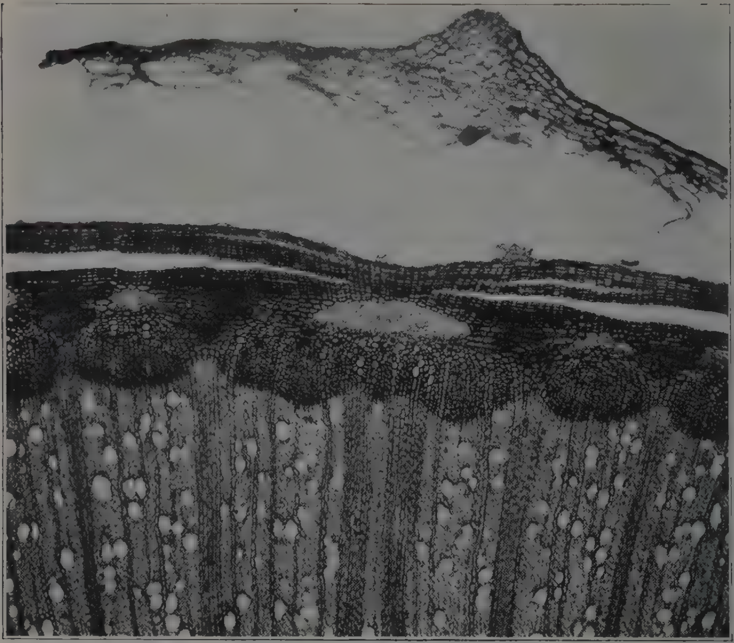

Fig. 9. Irregular Margin of the Xylem at the Base of a Cuthbert Cane

Sectioned just before bloom. Suggests the possibility that senile decline of the cambium begins sometime in the first season. ×96.

Figure 8 illustrates this condition at the base of a vigorous cane of the Cuthbert variety. In the Evergreen blackberry no cambial activity was noted in the basal region of the few canes examined, and no new xylem was formed in the second year. This condition is shown in Figure 10.

The slow response and feeble development may be considered indications of senile decline in the raspberry cambium. That this decline may begin toward the close of the previous growing season, is suggested by the irregular margin of the xylem in the dormant young cane (see Figures 9 and 20), altho some disturbance in relation to the kind or quantity of available food substances possibly may have produced this effect. This irregular development of the xylem areas between the aggregate rays was more noticeable in the Evergreen blackberry in the few canes examined, as shown in Figure 10. Altho the difference in radial growth of the xylem in these areas usually did not amount to more than 8 or 10 cells, it is considered possible that this difference is the result of earlier cessation of cambial activity in some areas. This somewhat erratic behavior of the cambium suggests the possibility that it was approaching the condition of senility, which is more evident in the old cane in the second season. Further evidence

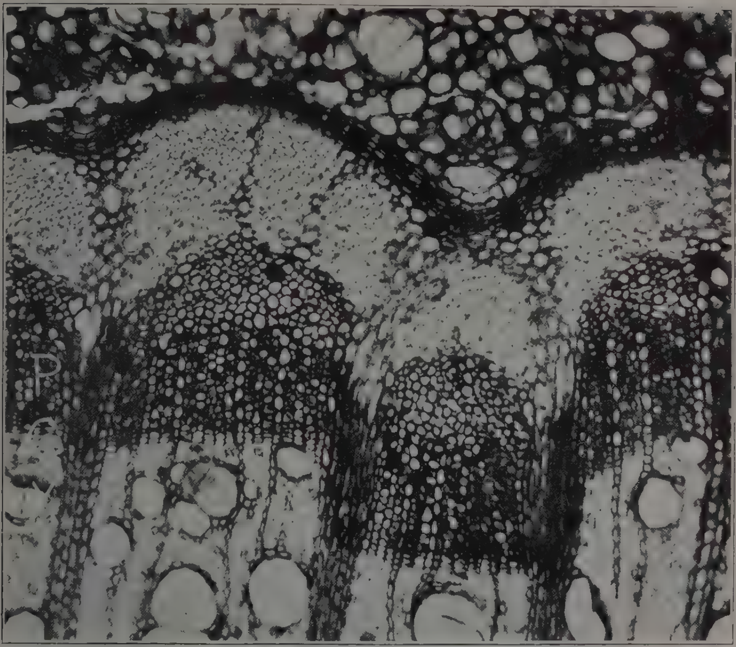

Fig. 10. Base of an Evergreen Blackberry Cane at the End of the Second Year

Shows resting cambium (C), wider area of active phloem (P) than in the red raspberry, and a markedly irregular margin of the xylem (X). No new xylem was formed. ×96.

of this decline will be presented in the discussion of the behavior of stem cuttings.

Development of New Xylem in the Old Cane

The most obvious result of cambial activity in the old cane in the second season is the formation of new xylem. That the old canes generally do increase in diameter in the central and tip regions but usually not at the base has been discussed. Studies of the anatomy of the old cane show the presence of new xylem in varying amounts in the regions which normally increase in diameter. The formation of new xylem elements was found to occur first just beneath a rapidly growing lateral and proceeded downward slowly from that point.

The amount of new xylem formed during the second season was much more extensive immediately below the laterals and on the same side of the cane. The areas of new xylem as seen in cross-section were greatly reduced or entirely absent on other sides of the cane (Fig. 12). This localized development often produced two, well-marked, but short ridges extending downward from the sides of the base of the lateral. Generally these "ridges" of xylem, which cor-

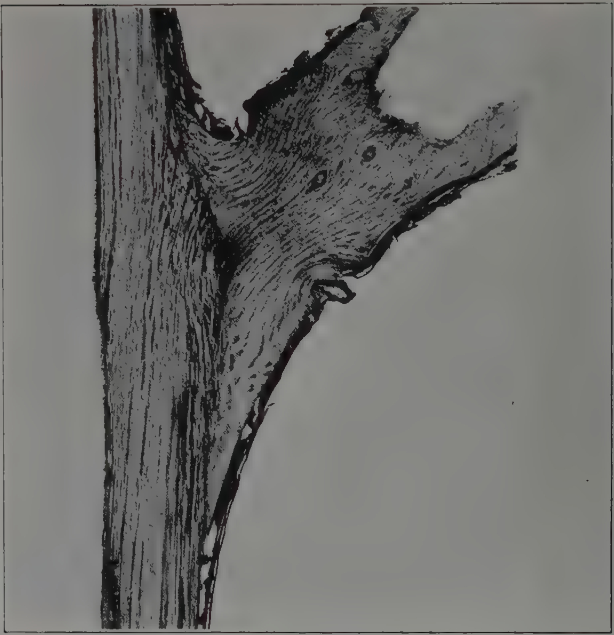

Fig. 11. Longitudinal Section Made in December Through the Base of a Lateral on a Vigorous Old Cane of the Latham Variety

"Wedge" of new xylem tapers to a point within 2 cm. below the point of bud insertion. Phloem in collapsed state. Pith and opposite side of old cane torn away in sectioning. ×6.

respond to the "wedges" described by Jost (13), continue for only a very short distance below the laterals. Figure 11 shows a longitudinal section through one side of a cane at the point of attachment of a vigorous lateral. This illustrates the rapid tapering of the wedges of new xylem. The distance from the point of bud insertion to the end of this wedge was not over 2 cm. The cross-sections shown in Figures 12, 13, 14, 15, and 16 were made at the base of a similar lateral, beginning at the point of bud insertion and progressing downward at 0.5 cm. intervals. These sections show the rapid narrowing of the wedges. The last of this series (Fig. 16), cut at a distance of only 2 cm. below the point of bud insertion, shows very narrow areas of new xylem in an incomplete ring.

The very limited development of new xylem at the base of the laterals provides a very weak attachment to the old cane and doubtless explains why the laterals are so easily broken off in cultivation and in picking, or in severe storms.

In canes which did not develop laterals close together, the stimulus

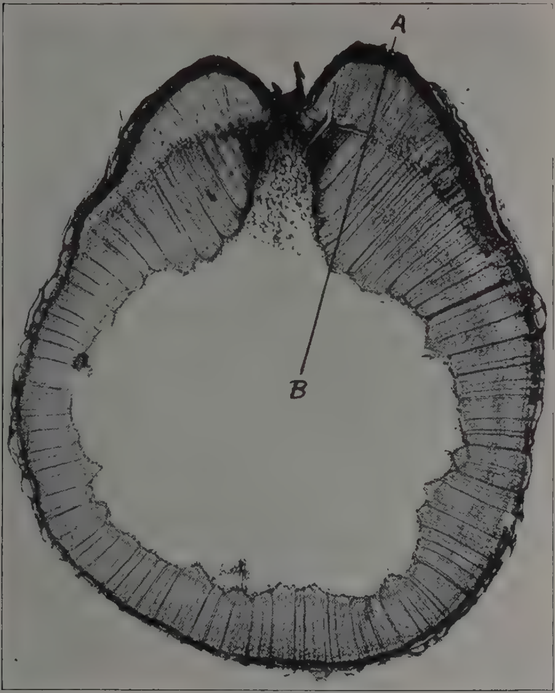

Fig. 12. Cross-section Through the Base of a Vigorous Lateral from the Same Cane as Figure 11

Section made at about the point of bud insertion. Note prominent "ridges" and the rapid narrowing of the area of new xylem. New ring incomplete. The line A-B indicates the approximate location of the section shown in Figure 11. ×6.

from the growing laterals apparently did not progress to any great distance down the cane. At the time of fruit-ripening, sections made 5 cm. below vigorous laterals often showed only a few scattered vessels and fibers, and in many cases there was no evidence to show that new xylem had been formed. Figure 17 shows a cross-section cut just beneath a lateral from a Cuthbert cane when the fruit was ripening. In this case new xylem was formed in some quantity at this point, but no evidence of new xylem formation could be found at a point only 5 cm. below.

When numerous laterals were developed fairly close together in the central and tip regions of a cane, the formation of new xylem was general around the cane. Altho a complete ring of new xylem may be formed under these conditions, as shown in Figure 18, this ring generally was very narrow and often was incomplete as shown in Figures 12 to 16. This very limited development of new xylem explains why

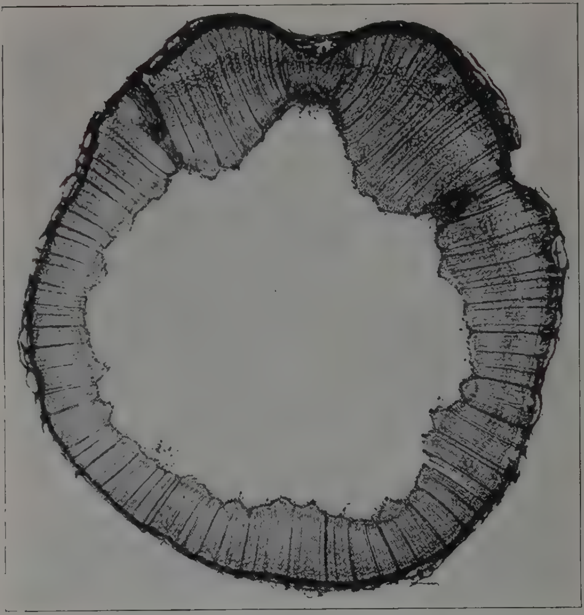

Fig. 13. Section Cut .5 cm. Below Figure 12. ×6

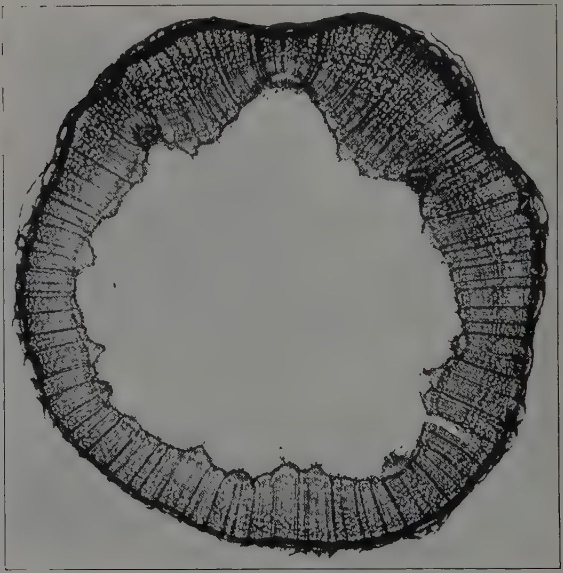

Fig. 14. Section Cut 1 cm. Below Figure 12. ×6

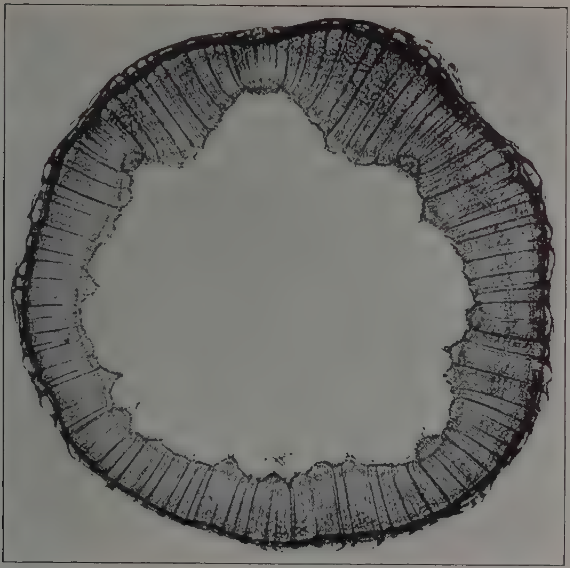

Fig. 15. Section Cut 1.5 cm. Below Figure 12. ×6

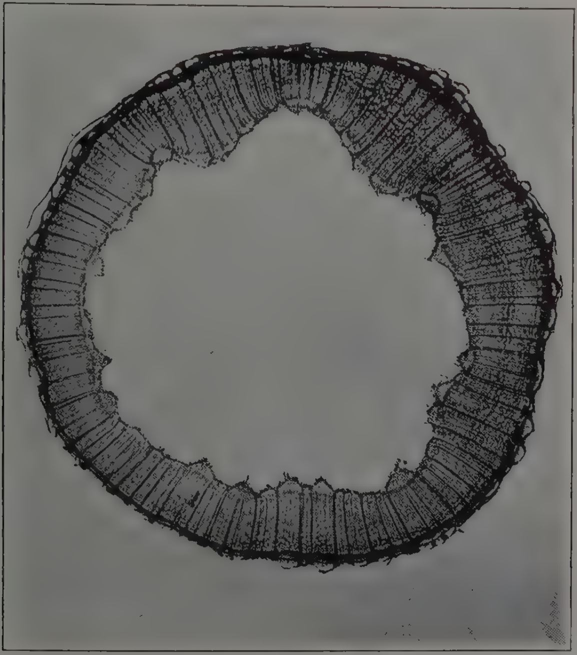

Fig. 16. Section Cut 2 cm. Below Figure 12. This and the Three Preceding Figures Show the Rapid Narrowing of the Wedges of New Xylem Below a Lateral. ×6

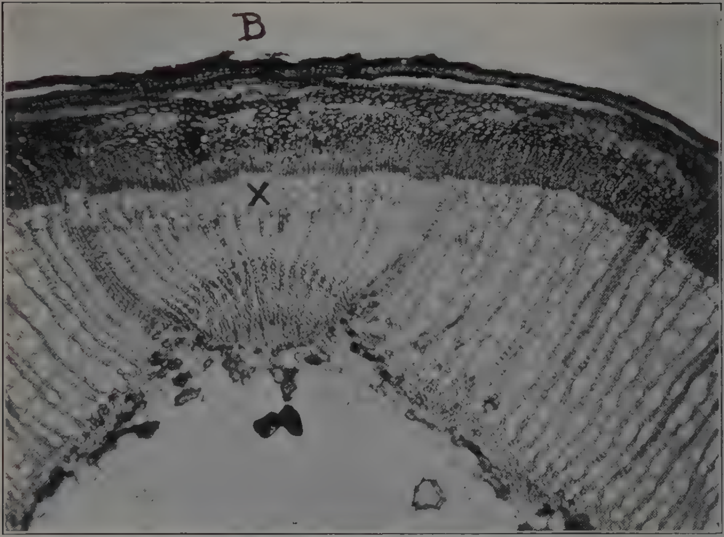

Fig. 17. Cross-section Made Just Below a Lateral of Medium Vigor in the Tip Region of a Cuthbert Cane

No other laterals within 15 cm. Fruit nearly all harvested. New xylem (×) in greatest area just below the point of bud insertion (B). "Ring" narrowing rapidly and absent over a large part of the opposite side of the stem. No trace of cambial activity 5 cm. below the lateral. ×96.

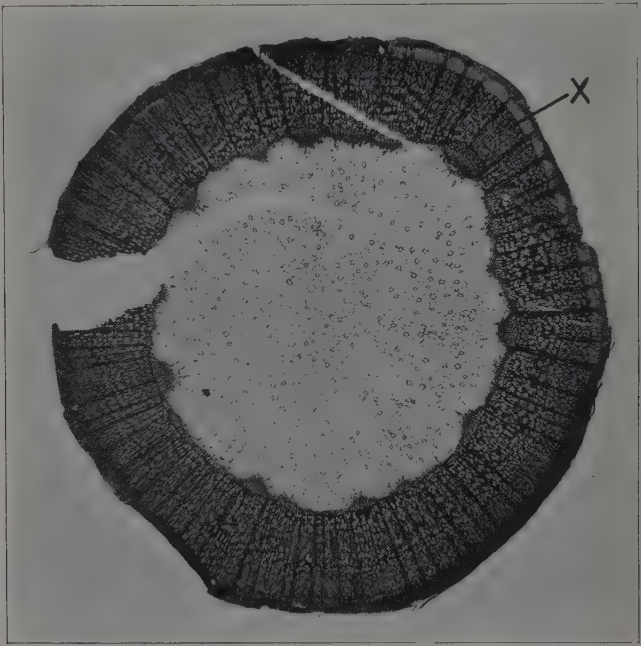

Fig. 18. Complete Ring of New Xylem (×) in Central Region of Latham Cane with Many Vigorous Laterals. ×6

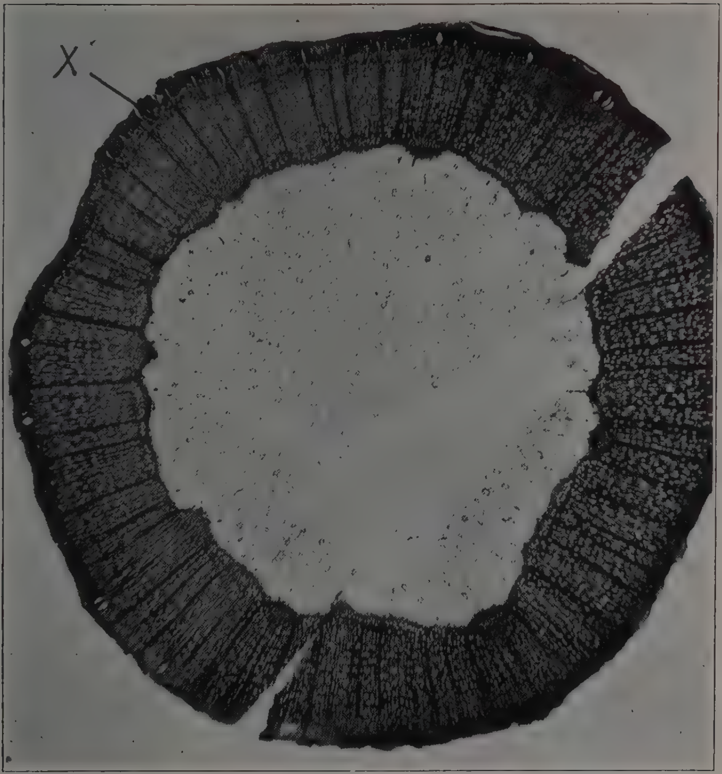

Fig. 19. Complete Ring of New Xylem (X) at the Base of a Latham Cane

Sectioned in November after the fruiting season. Several vigorous laterals were present in the basal region of this cane. X6.

there is such a slight increase in diameters throughout the length of the old cane. This slight increase occurred, however, even at the very tip of the cane, providing fairly well-developed laterals were present.

It is apparent from the foregoing evidence that the general, altho feeble, development of new xylem, which causes the increase in diameter in the upper regions of the cane, is caused by the cumulative effect of the stimulus from many laterals upon cambial activity.

The average cane does not produce many laterals in the basal region. Usually there are no laterals within 10 to 15 cm. from the ground. In the absence of basal laterals, the stimulus from laterals higher up on the cane apparently does not proceed downward far enough to affect the cambium at the base. Because this stimulus is lacking, the cambium at the base remains in a resting condition, or nearly so, and no new xylem is formed (Fig. 8). Without the formation of new xylem no measurable increase in diameter occurs at this point. However, when vigorous fruiting laterals developed in the basal region, as noted previously with regard to the performance of the Latham variety, new xylem was found in this region, but the area commonly was not extensive and the "ring" often incomplete. When these basal laterals were extremely vigorous, or when they were sterile and developed into new canes, the new xylem often formed a complete ring, which in some cases was of considerable width, as shown in Figure 19. This occurrance of new xylem explains the increase of diameter at the base in about 10 per cent of old canes.

Xylem formation has been shown to be more abundant just below a vigorous lateral than below a lateral of medium vigor. Some data obtained at the Minnesota Experiment Station, relating to the effects of pruning on cane behavior, show that canes pruned to a height of 36 inches produced longer and stouter laterals than canes pruned to a height of 60 inches. The shorter canes when examined showed a slightly larger amount of new xylem than the longer canes, but these shorter canes suffered more severely from storm damage to the laterals. In a series of plots, grown in staked hills and equally exposed to storm damage, the 36-inch canes showed an average of 12.9 per cent of the laterals broken off, whereas in the 60-inch canes the loss from breakage was only 9.2 per cent. It is apparent from these data that the increase in the vigor of the laterals on the shorter canes did not result in an increase in the strength of attachment to the cane sufficient to support the longer growth against the additional wind leverage.

Development of New Phloem in the Old Cane

The evidence obtained relative to phloem formation in the old cane is neither so clear nor so extensive as that relating to new xylem. Where new xylem was found in the old cane it was often accompanied by an area of phloem adjacent to the cambium, which stained noticeably darker, as shown in Figures 5, 17, and 20. This darker stain indicates that these cells are of more recent development with denser protoplasm than cells farther out in the phloem area. A more detailed study of these cells showed them to be filled with dense (heavily stained) protoplasm, whereas cells farther out were often empty. Some of the darker-stained cells may have been differentiated late in the previous growing season and remained in an active condition. This apparently is the condition also found in the Evergreen blackberry (Fig. 10). Others possibly were formed from the cambial initials late in the previous season, but were not completely differentiated until the start of the second year. Eames and MacDaniels (6) (p. 155) state in regard to the differentiation of phloem: "There is evidence to show that the cambial derivative cells first to mature in the

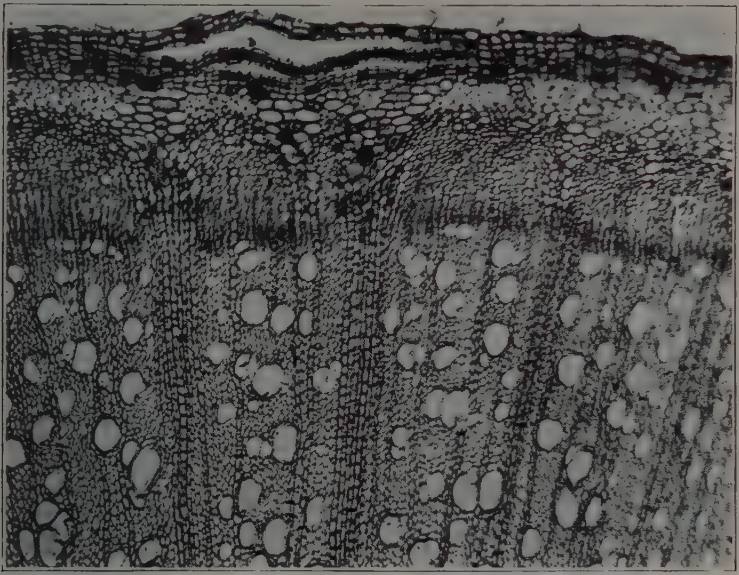

Fig. 20. Cross-section of Tip Region of Cuthbert Cane

Laterals 8-10 cm. long and blossom buds about ready to open. Cambium apparently inactive. Narrow area of phloem (P) adjacent to the cambium stained darker than remainder. Margin of xylem somewhat irregular. ×96.

spring are phloem mother cells. Of these, at least a part were cells which were cut off from the cambial initials during the previous season and have remained over winter in an immature condition." It has been shown already that the cambial area in some cases is reduced in width, altho the cambium showed no marked indications of activity (Figs. 7 and 8). This is considered evidence that some phloem cells are matured in the second year without division of the cambial initials at that time. Still others of the darker-stained phloem cells probably were the result of cambial activity in the second season.

Knudson (16) noted that in the grape and apple new xylem and phloem were formed simultaneously. This may also be the type of behavior in the red raspberry, as the darker-stained areas shown in Figures 5 and 20 appear to be wider than would be accounted for by the differentiation in the spring of a few immature cells cut off from the cambial initials at the close of the previous season. Altho the probability exists that the outer portions of this area may have been made up of cells which were differentiated late in the previous season and remained in an active condition, it is also probable that some of the innermost cells may have been formed by the division of cambial initials at the same time that new xylem cells were formed.

This phloem area regardless of time of formation was relatively narrow, being comparable in that respect to the narrow area of new xylem ordinarily found in old canes. As it appears probable that only a part of this narrow area was formed from the cambial initials in the second season, this may be considered further proof of the feeble activity of the cambium in the old canes.

Decline of the Phloem

Numerous examinations of old canes showed that the phloem began to break down at about the height of the harvest season. In Cuthbert plants, grown in the greenhouse, browning of the phloem at the base of the old canes was found to begin when about half of the fruits had ripened. In field-grown plants of King and Latham no discoloration was noted until most of the crop had matured. This discoloration occurred a little earlier in the season in the King than in the Latham, but the fruiting season of the King is also earlier than the Latham. Toward the end of August when the foliage of the old canes was beginning to turn yellow and terminal growth of the young canes had almost ceased, the browning of the phloem at the base of the canes was more noticeable. In early September the browning was more pronounced, but at that time there was no indication of collapse of the cells. The browning was intensified by the end of September, and, in canes examined in November after the leaves had fallen, the phloem was almost completely broken down and the cells were often collapsed. This condition is shown in Figures 11 and 21.

The breakdown of the phloem appeared to occur first at the base of the canes, a region in which little or no cambial activity in the second season was found. In the central region of the canes the phloem did not discolor until some time later than at the base. In many of the canes examined the phloem in this region was apparently normal in late August. Degeneration of the phloem in the tip region of the canes appeared to occur at about the same time as at the base. In some cases the tip region was the first to show this discoloration. This condition at the tips is thought to be caused by some disturbance in the water supply of the region, as that part of the cane often shows signs of drouth injury, while the lower portions are not affected as much. The cambium in the tip region has been shown to be fairly active, so it appears that the degeneration of the phloem in this region is not due to the same cause as degeneration at the base, where the cambium is inactive as a rule. Altho sectioning the material in the fresh condition made it difficult to determine the extent of tylose formation, nevertheless numerous indications of these growths were found at the base of the old canes. Whether these occur in sufficient

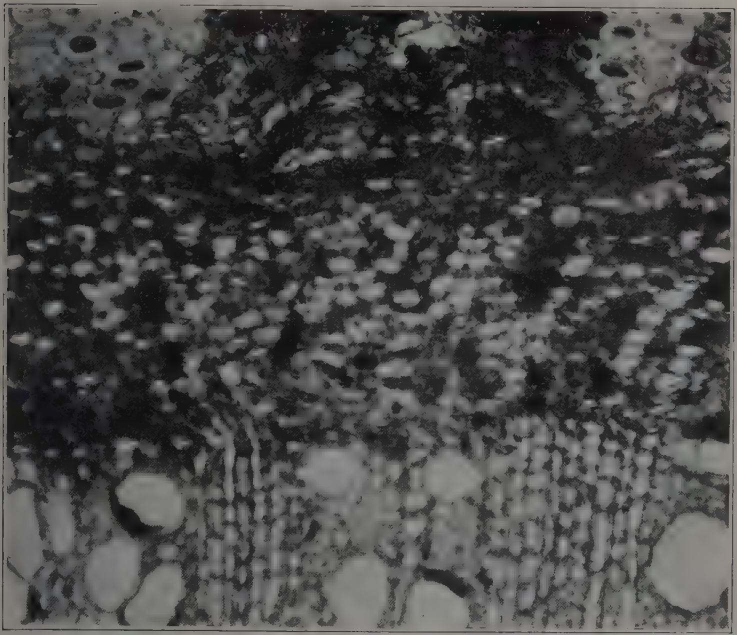

Fig. 21. Cross-section from the Base of a Ranere Cane Cut in January After the Fruiting Season. Complete Breakdown of the Phloem in the Dead Cane. ×435

numbers to interfere with water conduction has not been determined. Marshall (19) in some unpublished studies has shown that more water under moderate pressure may be forced through portions of old canes than through similar portions of new canes, but he has not shown that this greater rate of flow occurs in the normal water conduction of the old cane. Observations of the behavior of the tip region of old canes in the field indicate a deficiency in the water supply as shown by weak growth, small size of fruit, and early withering. Whatever the facts may be in relation to the water supply of the tip region, it is evident that the phloem of this portion of the cane declines at about the same time as that at the base.

Whether the degeneration of the phloem causes the decline of the old cane or vice versa has not been determined, but it is evident that phloem decline is at least associated with the death of the old cane. As phloem is known to be a relatively short-lived tissue and as the cambium in the old cane has been shown to be feeble, producing very little new phloem in the second year, it is possible that phloem decline in the raspberry cane is another expression of senility in the cambium.

Further evidence of decline in the phloem has been obtained through chemical analyses made in another phase of these studies of the raspberry cane. Some unpublished results of analyses made after harvest and in late November show the presence of reducing sugars in some quantity as the old cane declines and dies. These sugars were found to be more abundant in the central and upper regions of the cane than at the base and in somewhat greater concentrations in the laterals than in the cane. The presence of reducing sugar, a form of food easily transported in the normal living plant, suggests that the phloem which normally transports such food substances has declined in its activities. From such evidence it appears probable that there is little transport of elaborated foods to the root from the old cane after the harvest season, and that removal of the old cane at this time results in little or no loss of food supply to the roots.

BEHAVIOR OF STEM CUTTINGS

There have been very few reports of successful propagation of the red raspberry by means of stem cuttings and the successes reported have been with a hybrid form. Darrow (5) reported for the Van Fleet variety, a hybrid of *R. inominatus* x *R. strigosus*, the successful use of 2- and 3-eye cuttings buried an inch deep in flats provided with bottom heat in a greenhouse. Zimmerman (30) found that this variety could be propagated also by means of cuttings made from the new laterals early in the spring, but later[2] stated that old shoots did not respond similarly. In the present studies little or no success has attended efforts to propagate the Cuthbert and Latham varieties by means of cuttings.

Hardwood cuttings, made in January, 1929, from the basal, central, and apical regions of both vigorous and weak canes of the Cuthbert variety, were packed in moistened acid peat and kept in storage at 36° to 45° F. Under similar conditions cuttings of some plants such as grape and currant usually callous more or less freely, but after 17 weeks none of these raspberry cuttings showed even a trace of callous formation and no roots were developed.

Similar cuttings of the Latham variety were made in January, 1930, and placed in a cutting bed provided with bottom heat in a cool greenhouse. Comparable lots were placed in basic sand, in acid peat, and in a mixture of acid sand and acid peat. A few cuttings of the Beta grape and of a red currant variety were placed with each lot for comparison. When examined after 33 days most of the grape and currant cuttings were found to be well established or well calloused. None of the raspberry cuttings had rooted and only 14 per cent showed evidence of callousing. This callous formation generally was very

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[2] Personal correspondence, 1930.

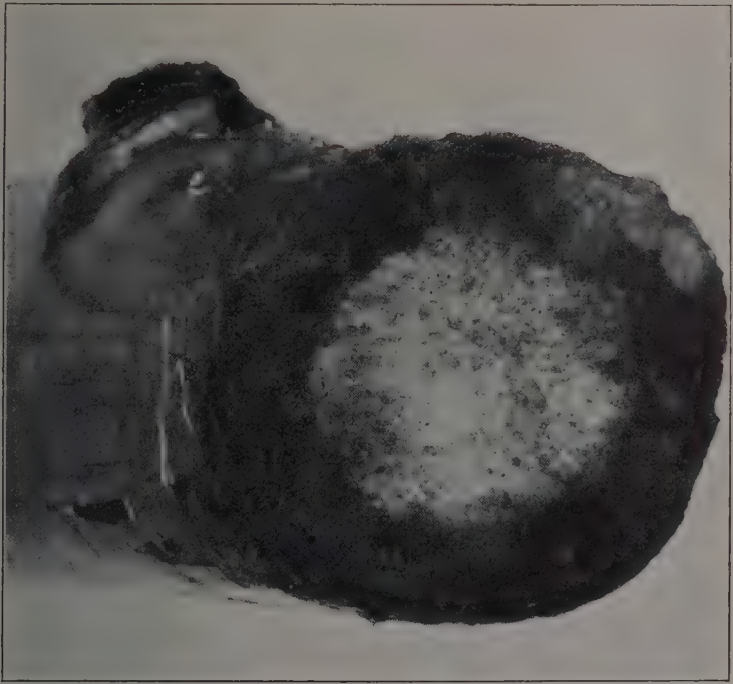

Fig. 22. Base of a Hardwood Cutting Made in January, 1930, from a Young Cane of Latham. After 33 days with Bottom Heat, Callous Formation Was Very Limited. × 5

feeble and at times was limited to a development on one side of the base of the cutting, as shown in Figure 22. More of those set in acid peat showed this feeble callousing than was the case in the other media, but all were failing rapidly. These data are given in Table IV. Altho the number of cuttings of each kind was not large the results as given in Table IV show that no regeneration of roots occurred in the red raspberry under conditions which brought about ready rooting in the grape and currant.

When sections were made of the cuttings which showed a feeble development of callous tissue, no indication of activity was found in the cambium at the proximal ends. Apparently the cambium in hardwood cuttings of the red raspberry does not respond as in the species studied by Sledge (26).

Some studies were also made relative to the callousing and rooting of green-wood cuttings of the Cuthbert and Latham varieties. Acid peat was used as the cutting bed medium and 200 cuttings of each variety were made in late April from the tips of young "suckers," which had grown 2 to 3 inches above the ground. Altho the losses

TABLE IV

Callousing and Rooting of Hardwood Cuttings of Red Raspberry, Grape, and Red Currant

Cutting bed medium	Latham raspberry		Beta grape		Red currant	
		No.		No.		No.
Basic sand	Leaves well developed, slight callous growth, no roots	1	Buds pushing, well calloused, rooting freely	7	Leaves well developed, well calloused, rooting freely	9
	Leaves withering, no callus, no roots	32	Buds pushing, well calloused, no roots	1	Buds dormant, well calloused, rooting freely	1
	Buds dormant, no callus, no roots	3	No bud activity, no callus, no roots	2		
Acid sand and acid peat	Weak bud activity, slight callous growth, no roots	1	Buds pushing, well calloused, rooting freely	10	Leaves well developed, well calloused, rooting freely	6
	Leaves withering, no callus, no roots	34			Buds swelling, well calloused, short root	1
	Buds dormant, no callus, no roots	2			Buds dormant, well calloused, no roots	3
Acid peat	Leaves withering, slight callous growth, no roots	13	Buds pushing, well calloused, rooting freely	9	Leaves well developed, well calloused, rooting freely	7
	Leaves withering, no callus, no roots	17			Buds pushing, well calloused, no roots	3
	Buds dormant, no callus, no roots	7				
		Per cent		Per cent		Per cent
Total rooting	0	0	26	90	24	80
Total callousing	16	14	1	3	6	20
Total failures	95	86	2	7	0	0

from damping off were heavy, in 12 days some feeble development of callous tissue was found in slightly less than half of the cuttings. In 33 days all of the Cuthbert and nearly all of the Latham cuttings had damped-off, but 9 fairly well rooted survivors remained among the Latham cuttings. This behavior suggests the possibility that a larger number of Latham cuttings would have rooted under more favorable conditions.

Another lot of cuttings was made from the tips of young canes of the Latham variety in late July, the canes at that time averaging 5 feet to 6 feet in height. These cuttings were set in acid peat in flats and kept outdoors in the shade. For 15 days they remained in good condition, but soon began to dry up or damp-off. Only 2 out of 200 cuttings showed any indications of callous formation and in these the callousing was very limited in extent.

Altho these studies of the callousing and rooting of raspberry stem cuttings were not extensive, they serve to indicate a very feeble response in the direction of regeneration of roots in the red raspberry. This response was more evident in the cuttings taken from very young suckers. By the end of July the response had declined markedly. In hardwood cuttings made from dormant young canes callousing was very feeble and no roots were formed. Priestly and Swingle (*22*) state that new root initials, when formed, are always found in tissues in close association with an active cambium. In view of this statement the fact that a few roots were formed on cuttings made from young suckers, but none on cuttings made later, seems to indicate that cambial activity declines in the cane during the first season and is feeble in the old cane. Evidence of this nature closely parallels that of the internal anatomy of the cane with regard to the behavior of the cambium.

CONCLUSIONS

The evidence obtained from these studies leads to the conclusion that the cambium in the red raspberry cane begins to decline in meristematic activity in the first season and is relatively feeble in the old cane. The apical meristem ceases to function at the end of the first season, no new winter buds are formed in the second year, and the cambium in the old cane forms relatively small amounts of new xylem and phloem elements. The evidence relating to the feebleness and decline of tissues within the old cane is in harmony with the decline of the cane as a whole, which has long been recognized by workers in the fields of botany and horticulture.

SUMMARY

Measurements of new and old canes show that there is an increase in diameter in the central and tip regions in the second year, but in 90 per cent of the old canes there is no measurable increase in diameter at the base.

The cambium during the first winter appears to be in a resting condition.

Cambial activity, as in other woody stems, is associated with the growth of new shoots.

Cambial activity, as shown by the formation of new xylem, probably occurs in nearly all growing canes in the second season. This activity in general is comparatively feeble and appears to be related to the vigor of the laterals and not to the vigor of the cane in the first year.

The formation of new xylem in the old cane does not appear to begin until the shoots have developed several leaves. In weak canes this activity is delayed and at times no new xylem is formed.

Cambial activity progresses downward slowly from the point of bud insertion and may be limited to the same side of the cane on which the shoot is growing.

Where the laterals are widely spaced on the cane the stimulus from the growing shoot does not appear to progress very far down the cane. In such cases the formation of new xylem may not occur 5 cm. below the shoot.

The limited development of new xylem at the base of the lateral usually results in a very weak attachment to the old cane and the lateral is easily broken off.

Where the laterals are numerous and fairly close together the cumulative stimulus from their growth results in general activity of the cambium and a complete tho narrow ring of new xylem is formed.

Apparently the stimulus from developing laterals does not extend downward far enough to cause the development of new xylem at the base of the average old cane, and there is usually no increase of diameter in that region of the cane.

Where vigorous laterals develop fairly close to the base of the old cane new xylem is formed. In some cases of this kind a complete ring of new xylem is formed. This explains the observation that in about 10 per cent of the old canes new xylem in varying amounts has been found at the base.

Cambial activity in neighboring areas between the large aggregate rays may not proceed at a uniform rate and some of these areas appear to cease growth earlier than others. This behavior suggests an early senile decline in the cambium.

Cambial activity in the second year is limited in some instances to the maturing of phloem initials cut off from the cambium late in the first year and to an increase in radial diameter of the remaining cambial cells. This condition is commonly found in the basal region of the old cane.

In the old cane, at about the height of the harvest season, discoloration of the phloem at the base of the cane indicates a breakdown of this tissue. Degeneration usually is more advanced in the basal region of the cane than in the central region. This degeneration is thought to be associated with the senile condition of the cambium.

Degeneration of the phloem in the apical region of the old cane, which is found to occur at about the same time as in the basal region, is believed to be caused by some disturbance in the water conduction in the old cane.

Studies of stem cuttings with regard to callous formation and regeneration of roots indicate that a decline in meristematic activity begins early in the first year.

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Agricultural Experiment Station
in co-operation with
Forest Service,
United States Department of Agriculture

Aspen
Availability, Properties, and Utilization

R. P. A. Johnson
Forest Products Laboratory
Joseph Kittredge, Jr.,
Lake States Forest Experiment Station
and
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CONTENTS

Page

Summary 5

Availability 7

Economic and silvicultural importance 7

Aspen and closely related woods 8

Aspen stands in the Lake States 9

Possibilities of aspen as a forest crop 22

Further information needed 24

Properties 25

General relation of properties to use of wood 25

Physical properties 27

Mechanical (strength) properties of wood 31

Decay resistance 39

Adaptability to the manufacture of pulp and paper 39

Characteristics depending on combinations of properties 40

Grading of lumber 46

Necessity for further research on properties 50

Utilization 52

History of use of aspen in the United States 51

The use of aspen in Europe 53

Lumber 53

Boxes and crates 57

Excelsior 60

Crossties 61

Fuel wood 63

Posts 64

Mine timbers 65

Slack cooperage 67

Tight cooperage 67

Page

Matches 67
Core stock 67
Novelties 68
Aspen in pulp and paper industry 68
Other uses of aspen 69
Extending the market for aspen 71

Conclusions 71

ILLUSTRATIONS

Page

Fig. 1. "Brush," five-year-old aspen, usually considered worthless 8
2. Aspen-paper birch forest, 50 years old, Superior National Forest 11
3. Well-stocked aspen, 20 years old, on good site, Chippewa National Forest, Minnesota 17
4. Well-stocked aspen, Superior National Forest, St. Louis County, Minnesota 18
5. Open stand of aspen, 45 years old, 8 inches average diameter, St. Louis County, Minnesota 19
6. The knots in aspen are characteristic of the species 28
7. Weight of air-dry aspen, 12 per cent moisture content, compared with the weight of several other species 29
8. Comparison of the average shrinkage of aspen with several other species 30
9. Average bending strength of the clear wood of aspen compared with several other species 31
10. Average compressive strength (endwise) of the clear wood of aspen compared with several other species 32
11. A comparison of the average shock-resisting ability or toughness of the clear wood of aspen with several other species 33
12. Average hardness of aspen compared with several other species 34
13. A comparison of the average stiffness of the clear wood of aspen with several other species 35
14. The nail-holding power of aspen compared with that of several other species 36

Page

Fig. 15. The loss of nail-holding power of aspen and several other woods when nails are driven into green wood and pulled after seasoning 37

16. Comparison of the splitting resistance of the clear wood of aspen with that of several other species 38

17. Characteristic joint failures in aspen glued with animal glue 43

18. Firsts and seconds and select aspen as graded under hardwood grading rules 47

19. No. 1 common and No. 2 common aspen as graded under hardwood grading rules 48

20. No. 3, No. 4, and No. 5 common aspen boards as graded under softwood grading rules 49

21. Types of aspen molding stock 55

22. Test panel of aspen siding, painted and unpainted, after ten months' exposure to the weather 56

23. Food containers made from aspen 58

24. Crates made from aspen....................................... 60

25. Aspen clothespins 68

ASPEN
AVAILABILITY, PROPERTIES, AND UTILIZATION

R. P. A. Johnson, Joseph Kittridge, Jr., and Henry Schmitz

SUMMARY

Aspen in Minnesota, Wisconsin, and Michigan occupies 21,000,000 acres, which is more area than occupied by any other forest type in the Lake States. Of this total acreage, 17,000,000 acres may be expected to produce merchantable yields. About 8,000,000 acres have stands averaging larger than 3 inches in diameter, and not more than 1,200,000 acres have stands averaging over 6 inches in diameter. The volume in stands over 3 inches in diameter is estimated at 29,000,000 cords of which about 12,000,000 cords are in stands over 6 inches in diameter. The volume will increase for 20 to 40 years owing to the large area of thrifty young growth that will become merchantable.

Aspen is a rapid-growing, short-lived tree and should usually be cut at an age of about 50 years. At that age small areas of well-stocked stands on average sites may be expected to yield 39 cords per acre, net scale. Over large areas the stands can be expected to yield between 5 and 20 cords to the acre, owing to openings and understocking.

The aspen tree is highly susceptible to decay. At 50 years of age about 10 per cent of the merchantable volume has advanced decay; in older stands the percentage is higher and in younger stands lower. In stands more than 50 years old, decay increases rapidly.

The stumpage value of aspen at present is low but it has been on an upward trend. Present prices range from 25 cents to $1 a cord, and from $1 to $2 per thousand board feet.

At present young stands of aspen are considered to be of little value. Large areas of 10-year-old aspen if held for 40 years, will earn about 4 per cent compound interest on the costs if the stumpage is then worth $1 a cord. This estimate of earning, which would be made by a company that plans to hold young growth for a future cut, is based on the most probable combination of ages, costs, site qualities, and stumpage values involved in growing a crop of aspen.

The clear wood of aspen has a number of excellent properties, the most desirable of which are softness, uniform texture, white color, light weight, ease of gluing, and low shrinkage. Aspen is as soft as basswood and softer than yellow poplar—two hardwoods noted for their softness. The exceedingly fine, uniform texture of aspen, combined

with softness, make it easy to work. Aspen wood weighs less than basswood and more than cottonwood, and of our native woods is one of the easiest to glue. Aspen shrinks less than basswood, but more than northern white pine. There are few hardwoods that do not swell and shrink more with changes in moisture content than does aspen. The combination of low shrinkage and straightness of grain permits aspen to stay well in place.

Compared with woods commonly used for structural purposes, aspen ranks low in most strength properties. It has the same bending strength as northern white pine but less than eastern hemlock. In stiffness and compressive strength (endwise), it is inferior to basswood but superior to northern white cedar. Aspen should not be used where bending or compressive strength is important.

Aspen is tough for a soft, lightweight wood; more so than basswood or yellow poplar, and as tough as eastern hemlock. The toughness of aspen is a desirable property in some of the uses to which lightweight, soft wood is put, but it does not adapt aspen to uses where toughness is the most important requirement.

Aspen wood has about the same nail-holding power as that of basswood and cottonwood. The softness and uniform texture of aspen, however, result in but little loss of nail-holding power from nails splitting the wood. Aspen is easily split with an ax owing to its straight grain and low strength across the grain. It splits with about the same ease as eastern spruce.

Aspen can be pulped by any of the standard processes. The yield of pulp per cord compares favorably with that of the commonly used softwoods. It is of an excellent color and is easily bleached, but is not as strong as pulp obtained from the softwoods commonly used.

The use of aspen for pulp is increasing. At present it is used principally for the production of soda pulp. Some is ground for newsprint. It can be used for the production of sulphite pulp, either alone or mixed with softwood.

Data on the use of aspen are meager and fragmentary. It is used almost everywhere it is found, but is cut in large quantities only in the Lake States. Information regarding the amount cut and its uses is difficult to obtain owing to the practice of statistical agencies of combining statistics on aspen with those on cottonwood.

A large amount of aspen is cut into lumber, which is used in the manufacture of many articles such as boxes, crating, and planing mill products. It is just beginning to be used for interior and exterior trim, flooring, planking, and for other building purposes. Except in a few industries, the species is almost unknown. Match, woodenware, and novelty manufacturers in the United States are experimenting with aspen, but in European countries it has been used for matches for many years. Aspen has been used successfully in the manufacture of clothes pins. Furniture and veneer panel manufacturers in the United States have not yet recognized the possibilities of aspen for core stock, but the adaptability of the wood to such use has long been recognized in Europe.

In considering the possibility of expanding the market for aspen lumber, past experience with other so-called little-used woods offers encouragement. At least three woods, now accepted and extensively used in the United States, were until a few years ago, in about the same state of development that aspen is.

Aspen is better known to users of wood in the form of logs, bolts, and like products than in the form of lumber. Manufacturers of excelsior accept it as one of the woods best adapted for high-grade excelsior. When treated with preservatives, it makes an acceptable crosstie in tracks not subject to heavy traffic. For years farmers of the Lake States have used it for fuel and for posts. Small amounts are used for mine timbers, principally in round form and some, for cooperage.

AVAILABILITY[1]

Economic and Silvicultural Importance

The abundance and importance of aspen, often called "popple," in the northern parts of the Lake States usually are not recognized because a large part of the supply is in young stands that have followed recent fires and consequently looks like brush rather than tree growth. (Fig. 1). Aspen occupies more area of forest land in the Lake States than any other tree species. It is estimated that aspen covers one third of the forest area in northern Michigan and two-thirds in Wisconsin and Minnesota. The merchantable volume in the existing stands is relatively small compared with the amount that will become available in the next 30 to 50 years. At that time, aspen will be a much more important source of raw material for wood-using industries than it is at present. A company that can adapt its manufacturing processes for the utilization of aspen within the next few years has every prospect of being able to obtain an abundant supply of raw material for many years.

Altho aspen has been, and still is, considered an undesirable species, there is no reason to believe that it will continue indefinitely to be regarded unfavorably. In the days of white pine logging, Norway pine, maple, and yellow birch were likewise considered undesirable.

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[1] The section which deals with the characteristics of the growth and stands of aspen, was written by Joseph Kittredge, Jr., senior silverculturist, Lake States Forest Experiment Station, St. Paul, Minn., except for the subsections and related species and on diseases, which were written by Henry Schmitz. Much of the material has been adapted from Minn. Expt. Sta. Tech. Bull. 60, "Forest Possibilities of Aspen Lands in the Lake States," in

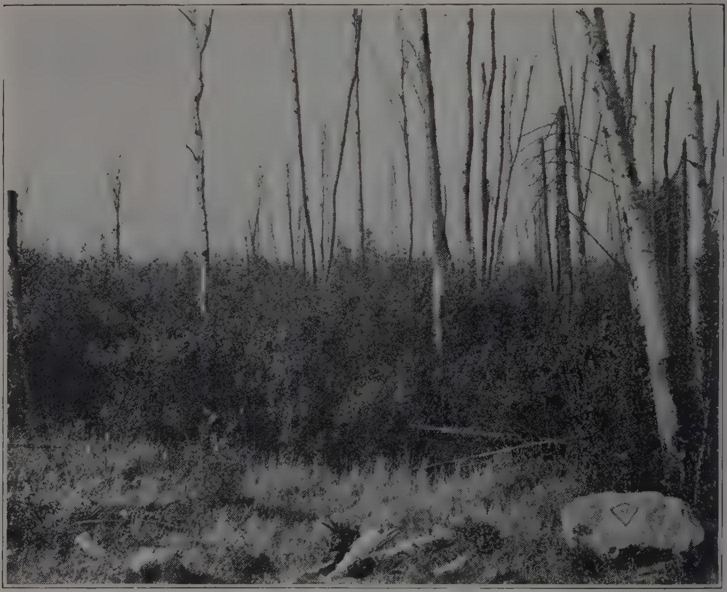

Fig. 1. "Brush," Five-Year-Old Aspen, Usually Considered Worthless

More recently hemlock was looked upon as a weed tree in the northern hardwood forest. Only a few years ago, jack pine was considered not worth cutting. Yet all of these species in turn have become marketable at prices that have justified large-scale commercial development. There is every reason to believe that aspen also will be cut and utilized to advantage. Aspen is useful and desirable for purposes other than the products it yields. It tends to maintain the forest soil in good condition. It serves as a nurse tree for the establishment of white pine and spruce reproduction. And finally, it provides its own fire insurance. Altho light fires will kill the part of the tree that is above the ground, the root system produces suckers prolifically after every fire and the new stand of suckers is more dense than the stand that was killed.

Aspen and Closely Related Woods

Aspens, together with cottonwoods and other poplars, not including yellow poplar, all belong to the genus *Populus*. In the Western Hemisphere, poplars are found from the Arctic Circle south to northern Mexico and Lower California, and from the Atlantic to the Pacific Coast. In the Eastern Hemisphere, poplars are found from the Arctic Circle to northern Africa, central China, and Japan.

In the more northerly parts of both hemispheres, the poplars form extensive forests. Chief among these are the aspen of North Amerca

(*Populus tremuloides*) and the European aspen (*Populus tremula*). The common North American aspen extends over approximately 112 degrees of longitude; the European, over 140 degrees; the two almost encircling the globe. Few trees have a wider distribution than these two species.

Aspens differ from cottonwoods in flower structure and not, as generally supposed, in the flattened leaf petiole. Many of the more common cottonwoods also have a flattened leaf petiole, a characteristic commonly ascribed to aspens.

Two species of aspen grow in North America. These are commonly known as aspen (*Populus tremuloides*) and large-tooth aspen (*Populus grandidentata*) and in the Lake States as popple or poplar. In the lumber and pulp industries, the two species are seldom separated. Several varieties of aspen (*Populus tremuloides*) are also recognized. The differences between the varieties are minor and of no concern to the lumberman, inasmuch as there are no distinguishable differences in the characteristics or properties of the wood.

Among the more important American relatives of the aspens are the swamp cottonwood (*Populus heterophylla*), balsam poplar (*Populus balsamifera*), northern black cottonwood (*Populus trichocarpa hastata*), eastern cottonwood (*Populus deltoides*), and cottonwood (*Populus sargentii*). The balsam poplar, or balm-of-Gilead, is the only one that grows extensively with the aspen in the northern part of the Great Lakes region.

Aspen Stands in the Lake States

Origin and life history of aspen stands.—In the old-growth forest, before cutting and slash fires, aspen must have been an uncommon and inconspicuous constituent of the forest. It probably occurred as an occasional small, suppressed tree, or group of trees, in the openings, particularly in the white pine and white spruce forests. As cuttings and fires removed the old growth and incidentally destroyed the few existing aspens, suckers came up from the roots in a radius of 25 or 30 feet around each of the stems that had been destroyed, and with 20 to 30 suckers to a stem. Every fire that burned over the area thus increased the density and the area of the aspen in the new crop. Almost all of the enormous area of aspen in the northern Lake States today has resulted from repetitions of this process.

The tiny "cotton"-tufted seeds of aspen are produced abundantly in most years on seed-producing trees. They are so light that it takes two or three million to make a pound; consequently they are carried long distances by the wind and germinate almost immediately if they fall on moist ground. Most of the seeds, however, never germinate, except in the occasional favorable season and place; or the frail seedlings die during their first year. Altho an insignificant part of the present aspen stands have originated directly from seed, seeding has been important in enabling the aspen to gain a foothold in new places so that scattered trees were widely distributed from which the suckers developed and spread as the old forest was removed.

The few seedlings which survive are likely to be destroyed by fire before they are 25 years old. The root systems are established, however, and a group of vigorous, rapid-growing suckers replaces each aspen that is killed. The new group occupies an area of about one fifteenth of an acre. Ten years later, more or less, the trees of this group are killed by another fire and the succeeding crop of suckers covers more than one fourth of an acre. After the fourth fire, the suckers from a single, original tree may completely and densely occupy an area of one acre. This process is significant because it could account for the presence of the aspen type on areas where aspen trees occurred at the rate of one per acre in the original forest and where four or more fires have burned subsequently. These two conditions have existed in the Lake States on very large areas, quite comparable with the area of the aspen type.

On small areas that escape fires, the aspen grows rapidly until about 50 years old. Many of the smaller trees are crowded out and killed in the competition in the dense stands. The fungus causing the common decay usually attacks the trees at or before this age. After 50 years, the decay increases, the vitality and growth of the trees decline, and few reach an age of 100 years. Some suckers start because the death of larger trees makes openings, but the suckers are usually few. Often balsam fir, pine, and spruce or maple and basswood replace the aspen at this stage and thus end the aspen cycle. More often it is renewed by cutting or fire in the early stages of development.

Present area.—The surveys of the Michigan Land Economic Survey, of the Wisconsin Economic Inventory, of Hansen in St. Louis County, Minnesota, of Sparhawk in Lincoln County, Wisconsin, and of the National Forests indicate that the aspen type occupies from one third to two thirds of the forest area in the northern Lake States. The total area has been estimated as 21,000,000 acres. A rough division of this area between the three states would give Minnesota 9,000,000, Wisconsin 7,000,000, and Michigan 5,000,000 acres. There is little evidence that the area of the aspen type will decrease appreciably in the next 50 years.

Distribution by sizes.—The existing surveys of a few counties indicate that 60 to 85 per cent of the aspen stands average from 0 to 3 inches in diameter, from 4 to 15 per cent between 3 and 6 inches, and from 0.1 to 11 per cent in stands more than 6 inches in diameter. These proportions vary in the different states and in different parts of the states. In the lower peninsula of Michigan there is less than 1 per cent of the aspen area covered by stands averaging more than 6 inches in diameter. In Minnesota as much as 10 per cent is probably occupied by such stands, and within areas like the National Forests which have been protected from fire, as much as 50 per cent. Wisconsin is probably intermediate between Michigan and Minnesota in this respect.

The manner of occurrence of the aspen of different sizes and different areas of stands is related to the history of the region. Aspen has come up most commonly on the former white-pine areas, which occupied a belt across north central Michigan, Wisconsin, and Minnesota. These areas were logged 30 to 50 years ago and a large proportion has since been taken up by settlers. Consuequently, aspen 30 to 50 years old is more commonly found in the white-pine belt in small units, frequently forming parts of farms. For this reason, it is not easy at the present time to find or block out large areas of aspen of merchantab'e size, altho there are such areas in places on old burns in northern Minnesota (Fig. 2). Likewise, young aspen, which has come up after recent fires and logging operations in the more northern parts of the region, occur in large areas where sizeable contiguous hold-

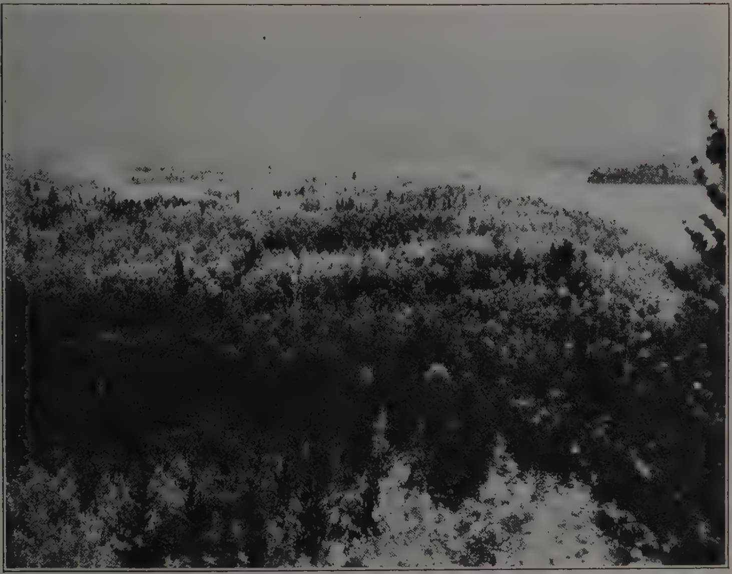

Fig. 2. Aspen-Paper Birch Forest, 50 Years Old, Superior National Forest
Occasional trees of jack pine, white spruce, and white pine in mixture.

ings could be acquired. Such areas would contain little merchantable forest now, but would serve primarily as a source of future supply.

It has been estimated that there are about 29,000,000 cords of aspen in trees 4 inches and more in diameter in the Lake States. A large proportion of this, however, is in trees 5 and 6 inches in diameter and progressively less in the larger sizes. At present most users of aspen do not utilize trees less than 6 inches in diameter. If an attempt were made to estimate the total amount of aspen in trees more than 6 inches in diameter, it would probably not exceed 12,000,000 cords.

The diameter classes from 0 to 3 inches, from 3 to 6, and more than 6 inches correspond to age classes from 0 to 25 years, 25 to 50, and 50 years and older. Aspen ordinarily reaches merchantable size in 50 years. The prediction can be made, therefore, that, altho there is less than 6 per cent of the aspen area in merchantable stands now, there will be from 15 to 40 per cent of the area that will become merchantable within 25 years, and the remaining 60 to 85 per cent will become merchantable in from 25 to 50 years. Not more than 20 per cent may die before reaching merchantable size. If the very conservative figure of 7 cords to the acre as an average stand, is used, it appears that the volume of aspen in 25 years will be 25,000,000 to 30,000,000 cords, and within 50 years more than 100,000,000 cords. These are very rough figures and make no allowances for cutting or decay, but they indicate how the present young stands will contribute to the volume that will be available in the future.

Diameters and heights attained.—The sizes of aspen at different ages vary with soil and site conditions; and the diameters, in particular, vary with the density of the stands. The average diameters that are attained in well-stocked stands in 40, 50, and 60 years on good, medium, and poor sites, are given in Table I. If 6 inches is considered to be the smallest average diameter at which aspen stands are merchantable, the figures indicate that, on sites of medium quality, the trees reach this average size in about 50 years; on good sites by 45 years; and on poor sites, not until after 60 years. If aspen is left to grow to old age, some trees may attain diameters of 12 to 15 inches and heights of 90 to 100 feet. Occasional trees are found with diameters as large as 20 inches.

TABLE I

AVERAGE DIAMETERS OF ASPEN IN WELL-STOCKED STANDS AT DIFFERENT AGES AND ON DIFFERENT SITES

Age	Average diameter breast high on		
	Good sites	Medium sites	Poor sites
Years	Inches	Inches	Inches
40	5.4	4.5	3.5
50	7.1	5.9	4.6
60	8.9	7.6	5.8

TABLE II

VOLUMES, IN CORDS, OF INDIVIDUAL ASPEN TREES, CORRESPONDING TO VARIOUS DIAMETERS AND HEIGHTS*

Diameter, breast high	Total height of tree, feet														Number of cubic feet of wood per cord†
	30	35	40	45	50	55	60	65	70	75	80	85	90	95	
Inches	Peeled volume ‡, cords														
4	.010	.013	.016	.019	.022	.026	028	032							58
5	.021	.025	.028	.035	.040	.045	.050	.055	.060						61
6	.034	.039	.045	.053	.060	.066	.073	.081	.088	.095					64
7			.062	.070	.079	.087	.096	.110	.110	.120	.13				68
8			.078	.089	.099	.110	.120	.130	.140	.150	.16	.17			71
9					.120	.130	.140	.160	.170	.180	.20	.21			74
10					.140	.160	.170	.190	.210	.220	.24	.26	.27		76
11						.190	.210	.230	.250	.260	.28	.30	.32		78
12							.240	.260	.280	.310	.33	.35	.37		79
13								.300	.330	350	.38	.40	.43	45	80
14									.370	400	43	.46	.48	.51	82
15									.420	.450	.48	.51	.54	.57	84
16									.470	.510	.54	58	.61	.65	85

* Basis, 477 trees. Block indicates extent of original data.

† Standard cords, 4 by 4 by 8 feet.

‡ Volume of peeled stem above a one-foot stump to a top diameter inside of bark of 3 inches. Compiled from the merchantable volume in cubic feet by dividing the volume per tree by the number of cubic feet per cord for each diameter. Eleven stacks of closely piled wood were measured to establish the relation between cubic feet and cords. Wood was cut and piled in 8-foot lengths.

TABLE III

VOLUME TABLE BY INTERNATIONAL LOG RULE* FOR SECOND-GROWTH ASPEN†

Diameter, breast high	Number of 16-foot logs								Basis
	1	1½	2	2½	3	3½	4	4½	
Inches	Volume ‡, board feet								Trees
6	15	20	26	31					43
7	15	24	32	40					42
8	15	27	39	50	60				47
9	15	30	44	58	74	90			37
10		34	51	68	86	104	122		36
11		37	58	79	100	120	144	167	22
12		41	66	92	118	144	171	198	26
13			75	106	138	170	202	233	23
14			83	123	161	199	237	274	18
15				142	185	230	276	319	5
16				163	213	264	319	369	
Basis	36	36	32	35	44	39	68	9	299

* Based on a ⅛-inch kerf.

† Block indicates extent of original data.

‡ Stump height, 1 foot; top diameter inside of bark, 5 inches; trees scaled in 16-foot lengths. Compiled by the frustum form factor method.

TABLE IV

VOLUME TABLE BY SCRIBNER DECIMAL C LOG RULE FOR SECOND-GROWTH ASPEN*

Diameter, breast high	Number of 16-foot logs								Basis
	1	1½	2	2½	3	3½	4	4½	
Inches	Volume †, board feet								Trees
7	2	3	4	6					20
8	2	3	4	6	7				47
9	2	3	5	6	8	9			37
10		3	5	7	8	10	12		36
11		4	6	7	9	11	13	15	22
12		4	6	8	10	13	15	17	26
13			7	9	12	14	17	20	23
14			8	11	14	16	19	23	18
15				12	15	19	22	26	5
16				14	17	22	26	30	
Basis	22	34	27	45	25	45	35	1	234

* Block indicates extent of original data.

† Stump height, 1 foot; top diameter inside of bark, 6 inches. Scaled in 16-foot lengths. Compiled by the frustum-form factor method from data collected in 1925.

The volumes of individual trees corresponding to different diameters and heights, in terms of a standard cord, are given in Table II. The volumes of trees in board feet by the international log rule, which approximates the volume obtained by careful sawing and close utilization to 5 inches inside bark diameter at the top, are given in Table III. The volumes in board feet by the Scribner Decimal C rule, with utilization to 6 inches top diameter inside bark, are given in Table IV.

Tables II, III, and IV can be used in estimating aspen stands by multiplying the volume given for cords or board feet, as desired, by the number of trees in the tally of corresponding diameters and heights. The figure for each diameter and height is an average and may not give the exact volume for an individual tree of that size, but when applied to about 25 or several hundred trees, such as are included in a cruise tally, it should represent closely the average volume of the trees of those dimensions.

Growth and yield of aspen.—Aspen grows rapidly; in fact, it is one of the most rapid growing species in the Lake States for the first 50 years, or until the age at which it reaches merchantable size. The rate of growth varies, however, with the soil and site conditions, and with the age of the stand. For example, on a medium site at 30 years, well-stocked stands grow at the rate of about 4/10 of a cord per acre annually, and at 50 years almost 9/10 of a cord, after which the average annual growth diminishes. On a good site at 50 years, the growth rate may be as much as 1¼ cords per acre annually, and on a poor site as little as 1/10 of a cord. These figures must, of course, be reduced to allow for defect and for openings in the stands, which always decrease the yields per acre over large areas.

TABLE V

CORDWOOD YIELD FOR WELL-STOCKED ASPEN IN TREES FOUR INCHES AND OVER IN DIAMETER, BREAST HIGH

Kind of site	Age	Average total height of dominant trees	Average diameter, breast high	Basal area per acre	Peeled volume per acre*
	Years	Feet	Inches	Square feet	Cords†
Good	20	40	2.9	83	5
	30	51	4.2	102	25
	40	62	5.4	120	43
	50	70	7.0	133	55
	60	76	9.0	144	63
	70	82	10.9	151	67
	80	86	12.6	155	69
Medium	30	44	3.5	94	12
	40	53	4.5	110	30
	50	60	5.9	122	44
	60	66	7.6	133	51
	70	70	9.3	139	55
	80	74	10.6	143	57
Poor	40	44	3.5	88	11
	50	50	4.6	98	26
	60	55	5.8	105	33
	70	59	7.1	109	37

* Stump height, 1 foot; top diameter inside of bark, 3 inches.

† Standard cord, 4 by 4 by 8 feet. Close piling. Volumes in cords were obtained by applying the factors used for conversion of merchantable volumes in cubic feet to cords to corresponding average diameters at breast height. As a check, the same results were obtained from curved distributions of stems of different sizes per acre for a given age. These latter curves were also used for obtaining volumes in cords for stands with average diameter less than 4 inches.

The yields of well-stocked stands of aspen at different ages and on good, medium, and poor sites, in board feet by the International and Scribner Decimal C rules, and in cords are given in Tables V, VI, and VII. (See also Figs. 3 and 4.)

TABLE VI

YIELD OF SECOND-GROWTH ASPEN IN TREES SIX INCHES AND OVER, INTERNATIONAL LOG RULE*

Kind of site	Age	Trees per acre, 6 inches and over	Average height	Average diameter, breast high	Basal area per acre, 6 inches and over	Volume per acre†
	Years	No.	Feet	Inches	Square feet	Board feet
Good	30	170	63	6.0	33	3,800
	40	319	66	6.7	80	9,200
	50	403	70	7.6	124	16,700
	60	320	76	9.0	143	23,700
	70	235	82	10.9	151	30,100
	80	180	86	12.6	155	34,800
Medium	30	80	59	6.1	14	1,400
	40	215	60	6.3	45	5,000
	50	358	62	6.9	96	10,700
	60	378	66	7.9	127	16,500
	70	290	70	9.3	138	21,300
	80	234	74	10.6	143	24,800
Poor	40	74	53	6.1	13	1,400
	50	200	54	6.4	42	4,500
	60	306	55	7.0	81	8,200
	70	327	59	7.6	102	11,500

* Based on a ⅛-inch kerf.

† Stump height, 1 foot; top diameter inside of bark, 5 inches. Bark is not included in volume.

TABLE VII

YIELD OF SECOND-GROWTH ASPEN, TREES SEVEN INCHES AND OVER, SCRIBNER DECIMAL C LOG RULE

Kind of site	Age	Trees per acre 7 inches and more	Average height	Average diameter, breast high	Basal area per acre	Volume per acre*
	Years	No.	Feet	Inches	Square feet	Board feet
Good	30	35	69	7.3	10	500
	40	167	70	7.6	52	3,400
	50	297	72	8.1	103	9,600
	60	290	77	9.3	135	17,300
	70	235	82	10.9	150	23,600
	80	180	86	12.6	154	27,400
Medium	40	68	65	7.5	21	1,000
	50	213	66	7.7	69	4,300
	60	300	68	8.3	112	10,300
	70	268	71	9.5	132	16,400
	80	229	74	10.6	140	19,700
Poor	50	68	58	7.4	20	1,000
	60	174	59	7.6	55	3,200
	70	240	60	8.0	84	6,600

* Stump height, 1 foot; top diameter inside bark, 6 inches. Bark is not included in volume.

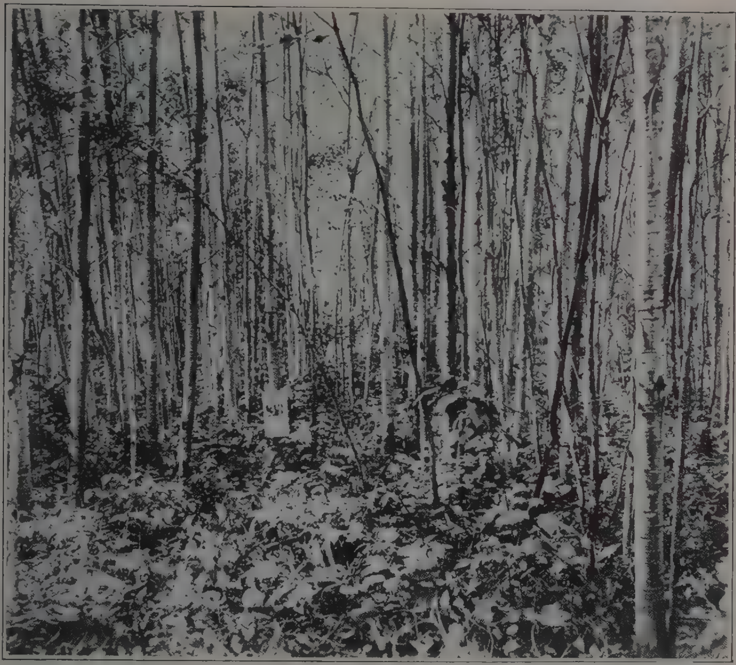

Fig. 3. Well-stocked aspen, 20 Years Old, on Good Site, Chippewa National Forest, Minnesota

If an average diameter of 6 inches is again taken as the merchantable limit, Tables V, VI, and VII show that well-stocked aspen on medium sites at 50 years will produce 44 cords to the acre in trees 4 inches and over, on good sites about 50 cords in 45 years, and on poor sites not more than 33 cords in 60 years. In board feet by the International rule, the corresponding figures are 10,000 board feet per acre at 50 years on the medium site; 13,000, at 45 years on the good site; and 8,000, at 60 years on the poor site.

The number of trees per acre from which these yields are obtained are also indicated in the tables. It is, of course, possible to obtain reasonably good yields at younger ages where the number of trees of merchantable size is correspondingly less. At 50 years on the medium site, when the trees average about 6 inches in diameter, only 358 out of 645 trees on the acre were 6 inches and more in diameter. The table for cordwood yield gives the number of trees over 4 inches in diameter, and the one for board feet by the Scribner rule, the number over 7 inches.

Over an area of 40 acres or more, there will be openings where the trees do not stand so thick and uniform as they did in the stands from

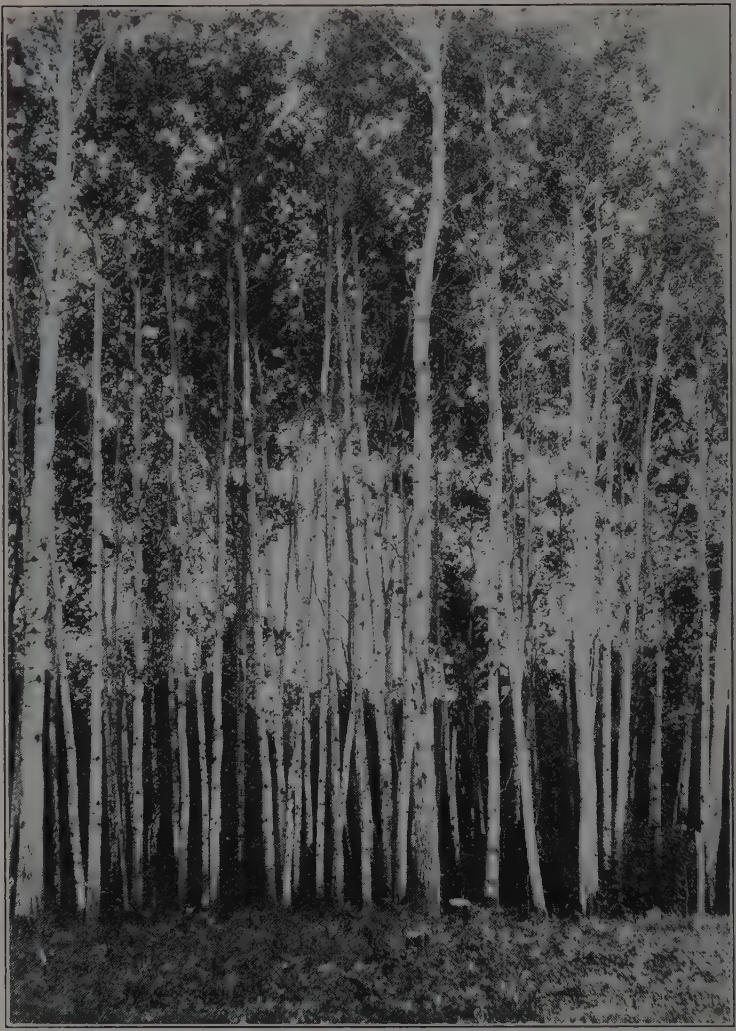

Fig. 4. Well-Stocked Aspen, Superior National Forest, St. Louis County, Minnesota

which these tables were made (Fig. 5). A cruise or estimate will indicate how much the volume per acre of any specific area falls below that given in the yield tables. A few figures from surveys of large areas will indicate how the stands may vary. A township in northern Minnesota had 11,006 acres which averaged 4½ cords to the acre; 32,000 acres in Bayfield County, Wisconsin, averaged 9½ cords per acre; 28,000 acres of aspen type on the Chippewa National Forest averaged 11 cords per acre; 1,223 acres in Bayfield County had a stand of 17 cords per acre, including the trees 3 inches and more in diameter. It is evident that aspen stands over large areas have less than half the yields indicated by the tables. It is estimated that more than two thirds of the aspen area is not well stocked and will produce smaller yields than indicated in Tables V, VI, and VII.

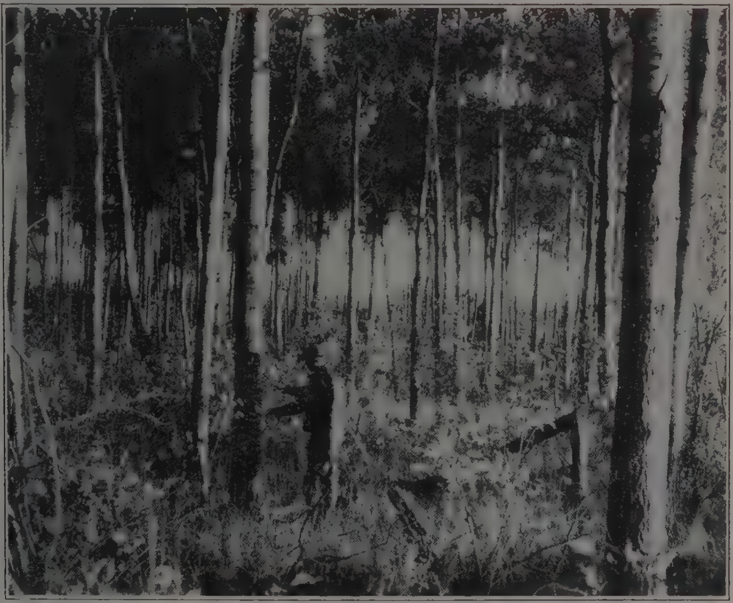

Fig. 5. Open Stand of Aspen, 45 Years Old, 8-Inch Average Diameter, St. Louis, County, Minnesota

Allowance must also be made in most cases for the defect caused by the fungous disease common in aspen stands. On an average site the decay caused by this disease at 40 years amounts to 7.8 per cent of the volume, at 50 years, 11.4 per cent; at 60 years, 15.7 per cent; and at 70 years, 20.5 per cent. The yield-table figures should be reduced accordingly to obtain the yields of sound wood, unless it is known definitely on a specific area whether the decay is more or less serious than that indicated by these percentages.

Ages of trees at maturity and rotation.—The average annual growth of aspen reaches a maximum at about 50 years. From then on the rate of growth decreases and the decay increases. It is therefore unwise to hold the stands to older ages if they will produce good merchantable yields at 50 years. Large yields of pulp wood on the medium and good sites will ordinarily be produced in 50 to 60 years, but large yields of saw timber, such as may be cut from stands 70 years old, are likely to be obtained only on sites better than medium. From 15 to 20 per cent of the aspen area in the northern part of the Lake States is on poor sites from which a satisfactory yield of merchantable aspen will rarely be obtained.

Diseases of aspen.—Aspen is highly susceptible to a number of diseases. These may be grouped as: (1) those affecting the leaves; (2) those affecting the twigs, branches, and the trunk; and (3) those attacking the wood of standing trees.

One of the most common and widespread leaf diseases of aspen is caused by *Sclerotium bifrons* E. and E. The disease is characterized by the eventual death of the entire leaf. Under certain conditions, as much as one half of the entire foliage of a tree may be killed. The dead leaves are usually persistent until autumn. The disease is very common in the southwestern stats, and has also been reported as occurring in the northern Rocky Mountain region, New England, the Adirondacks, and Wisconsin. Altho no detailed study seems to have been made of the effect of this disease on the rate of growth of aspen, it must be appreciable if the infection is heavy.

Another common and important leaf disease of aspen is caused by a fungus usually referred to as *Marsonia populi* (Lib.) Sacc. This disease is reported as the cause of a blight in the Rocky Mountain region from Colorado to Idaho. It also occurs in New England and in the Lake States, but apparently is seldom the cause of great damage.

The young shoots of aspen are often affected by a disease that causes them to turn almost a jet black and to bend back. The petioles of leaves attached to such twigs also become blackened and portions of the leaves may be similarly affected. The disease is believed to be caused by the fungus *Napicladium tremulae* (Frank) Sacc. It is not yet certain, however, that a somewhat similar condition may not be caused by other organisms. The disease is widespread and occurs practically throughout the range of aspen.

At least four fungi are known to cause cankers of the branches and the main trunk of aspen. Two of these are of European origin, and one of the two is known to occur in the United States.

By far the most common canker of aspen in the Lake States region is caused by *Cytospora chrysosperma* (Pers.) Fr. Cankers caused by this fungus are characterized by the reddish yellow spore horns which give them a bewhiskered appearance when the spores are produced.

Another important canker of aspen in the Lake States is caused by *Hypoxylon pruinatum* (Klotsche) Cke. Cankers caused by this fungus are usually confined to the trunk, and eventually kill the tree by girdling it. As it has not been reported on trees more than 6 inches in diameter, this disease would seem to be confined to comparatively young trees.

A study[2] of *Hypoxylon* canker in the Lake States showed 37 per cent of the trees on sample plots infectd, and 37 per cent killed by the disease. How prevalent this type of canker is in the Lake States region is not known.

A canker occurring on aspen is of importance, irrespective of the specific cause, as it may eventually lead to the death of the tree or be the means of entry for wood-destroying fungi.

By far the most important group of diseases affecting the utilization of aspen are those that cause the wood of standing trees to decay. Altho a large number of wood-destroying fungi have been reported as occasionally occurring on aspen, two fungi, the false tinder fungus (*Fomes igniarius*) and the butt-rot fungus (*Fomes applanatus*) account for practically all of the rot ordinarily found in this tree.

Altho *Fomes igniarius* is the cause of a heart rot and *Fomes applanatus* is characteristically the cause of butt rot, it is not necessary to consider separately the losses caused by them. For all practical purposes there is no important difference in their effects on the chemical and physical properties of aspen wood.

Three stages of decay are arbitrarily distinguished: (1) incipient, (2) intermediate, and (3) final. The incipient stage of decay is of little importance, as it is seldom recognized and never culled by any industry using aspen. The intermediate stage includes all variation in color from straw to chocolate brown, but the wood is apparently still hard and firm. This stage of decay is recognized as a defect in aspen lumber, but for many uses the utility of the wood is not seriously impaired. The final stage of decay includes all soft, punky wood, irrespective of color. This stage of decay is considered as a serious defect and is culled by all industries using aspen.

At 70 years of age, the total rot, namely, incipient, intermediate, and final, affects 31.2 per cent of the merchantable volume of the tree; at 60 years, 27.5; at 50 years, 23.0; at 40 years, 18.9; and at 30 years, 14.8 per cent. At 70 years the intermediate and final stages of decay include 20.5 per cent of the merchantable tree volume; at 60 years, 15.7; at 50 years, 11.4; at 40 years, 7.8; and at 30 years, 4.8 per cent.

The figures must not be taken too literally, and they can not be applied with exactitude to a specific area. They indicate only the proportion of decay which, on an average, might be expected in aspen in Minnesota. They also indicate the desirability, at least from the standpoint of heart rot, of growing aspen under a 40- to 50-year rotation.

The study from which the foregoing percentages were obtained was made in "wild" stands. Under forest management, injurious factors which have contributed to the defective condition of the present stands will undoubtedly be materially reduced. Fire is the most important of these injurious factors, because fire scars offer an excellent means of entry for wood-destroying fungi. Mechanical injuries, canker, and insects are also important causes.

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[2] Poran, A. Hypoxylon, poplar canker. Phytopath. 14:140-145. 1929.

Stumpage values.—The value of standing aspen depends upon many factors, including not only the amount and quality of the aspen, but its location with respect to roads, railroads, or manufacturing plants. The prices which have been paid for standing aspen during the last few years vary from 25 cents to $1 per cord and from $1 to $2 per thousand board feet. There are still many areas of aspen, however, that are so located that the owners are unable to sell them at any price. As the use and demand for aspen increases, more of the stands that at present are not salable will become marketable and the average stumpage value which may now be between 50 cents and $1 a cord will tend to increase.

Possibilities of Aspen as a Forest Crop

As a forest crop for the repeated or permanent production of wood products, aspen offers several marked advantages. It is one of the easiest trees to reproduce after cutting. It is only necessary to cut as clean as possible, and during the first two seasons, following the cutting, a dense crop of rapidly growing aspen suckers is assured. On land that produced a merchantable yield at the time of cutting, the suckers may be expected to grow and after 50 years again to provide a good yield. Often the aspen stands are extremely dense suggesting that their growth may be retarded. The larger trees forming the crop at maturity, however, seem to be only rarely seriously retarded. Thinnings might stimulate the growth somewhat in dense stands. At the ages of 15 to 30 years when the thinnings would be most beneficial they will not provide any return in the form of marketable products for the cost of making them. The possible later return induced by increased growth has not yet been demonstrated.

The most interesting and practical suggestion for those who are considering aspen as a forest crop is the possibility of acquiring areas of young growth for a future supply. It has been shown that the aspen lands in the Lake States include a large proportion of stands less than 3 inches in diameter, and from 5 to 20 years old. This young aspen is now considered to have little or no value. It is growing rapidly, however, and will produce a good yield at least of cordwood products when it is 40 to 50 years old. The acquisition of land, with young growth already established, means, therefore, reducing the period, during which the land must be held and taxes paid, by a number of years corresponding to the present age of the young growth. The cost of holding land for a forest crop 20 years, as compared with 40 or 50 years, obviously is much less. The fire hazard in holding the young stands is not so great as would be that on freshly cut-over areas, and in case of destruction by fire, only the growth for the period corresponding to the age of the young stand is lost.

Altho aspen grows on some excellent agricultural soils, there are also large areas on rough or stony soils that have little or no value at present, as indicated by the large areas of land of this type that are added to the tax-delinquent rôles each year. In the following calculations, the aspen lands have been given a value of $2 an acre, altho many areas of aspen could not be sold at that price. Any reduction of the land value would increase the figures of profit given below. The expenses of holding aspen lands have been placed at 10 cents an acre a year—the figure adopted in the Wisconsin forest tax law—with an additional 3 cents per acre per year for special protection by the owner aside from that provided by the state. With these assumptions, figures of the interest returns from growing aspen crops for different combinations of yield per acre, growing period, and stumpage values after a 10 per cent yield tax has been deducted, are presented in Table VIII.

TABLE VIII

COMPOUND INTEREST EARNED ON INVESTMENTS AND COSTS OF GROWING ASPEN IN RELATION TO YIELDS AND STUMPAGE VALUE*

Growing period	Yield per acre	Stumpage value per cord less 10 per cent yield tax				
		$0.45	$0.90	$1.35	$1.80	$2.25
Years	Cords	Compound interest rate				
30	5	loss	0.3	1.9	3.0	3.9
30	10	0.2	2.9	4.5	5.6	6.5
30	20	3.0	5.6	7.1	8.2	9.1
30	30	4.5	7.1	8.7	9.8	10.7
40	5	loss	loss	0.7	1.6	2.3
40	10	loss	1.6	2.8	3.7	4.3
40	20	1.6	3.7	4.9	5.8	6.4
40	30	2.8	4.9	6.1	7.0	7.7
50	10	loss	0.9	1.9	2.6	3.1
50	20	0.9	2.6	3.6	4.2	4.8
50	30	1.9	3.6	4.6	5.3	5.8
50	40	2.5	4.2	5.2	6.0	6.5

* Land value, $2 an acre; annual expense, 10 cents for taxes plus 3 cents for protection.

Table VIII can be used in several ways. The increased profitableness of selecting and holding aspen lands that are accessible and, therefore, have higher stumpage values, but that have good stands that will produce high yields is obvious. For example, an area so located that its stumpage will be worth $2 a cord and that will produce 20 cords to the acre after 30 years, will yield more than 8 per cent interest, whereas one on which the stumpage value is only 50 cents a cord and that will produce only 10 cords to the acre will yield only two tenths of 1 per cent interest. The higher yield results, of course, on areas of good site quality and where the trees stand thickly. These points have been brought out in the discussion of growth and yield. A further advantage appears in the reduction of the length of the growing period, an advantage inherent in a good site quality and one that may also be obtained by acquiring at low prices aspen which is already 10 or 20 years old, and by that number of years nearer to merchantable size. In Table VIII, if a yield of 20 cords to the acre and a stumpage value of $1 a cord are assumed, a stand which can be cut in 30 years will earn 5.6 per cent interest, whereas one which must be held for 50 years will earn only 2.6 per cent interest. Another use of the table can be made by anyone who wishes to set the interest which his aspen lands must produce, and on that basis decide what kinds of land and stands he will buy or hold. If he estimates that aspen will be worth $1.50 a cord (equivalent to $1.35 as shown in column 5, Table VIII) and 5 per cent is the minimum rate of interest that he is willing to accept, the table indicates that the aspen stands must yield at least 12 cords in 30 years or 21 cords in 40 years, or 37 cords if it is necessary to hold them for 50 years. Looking at it in another way, if it appears that a yield of only 10 cords to the acre can be obtained, then to earn 5 per cent, the stumpage value after 30 years must be about $1.75 per cord, and after 40 years, more than $2.50 per cord.

In general, considering the large proportion of well-stocked aspen stands already 10 to 20 years old which may be expected to produce 20 cords to the acre when they are merchantable, interest rates earned by the growth of such stands, even at present stumpage values, are mostly above 4 per cent.

Further Information Needed

Further information needed may be summarized as follows:

1. At what ages on different qualities of site, and especially on the poor qualities, does aspen deteriorate and the stands die before reaching merchantable size?

2. Are there any means by which the decay in aspen from the prevalent fungous disease can be prevented or minimized in a practicable way?

3. The collection of information currently by the census or other agency on the stumpage values of aspen separately from those of cot-

tonwood, poplar, or other species, should be undertaken and included in published reports.

4. Better and more complete information is needed as to the locations, age classes, site qualities, and stands per acre of aspen in the region. Some of this information is being obtained in certain counties by the state land economic surveys. Their work should be encouraged, and expanded and supplemented to provide more nearly complete information.

PROPERTIES[2]

General Relation of Properties to Use of Wood

The clear wood of aspen has inherent properties of merit. Several of these properties are familiar to a large proportion of the general public, for some of the common types of matches are made of this wood. The requirements of wood for matches are exacting in that the wood must combine straightness of grain, ease of splitting, ease of working, and toughness. To meet such rigid requirements, a wood must be suitable for other uses as well. The fact that aspen is not used more widely for other purposes lies not in the wood itself but in other factors, such as cost, distribution of stand, and availability in desired sizes and grades. Cost, demand, and harvesting and marketing practices change as conditions change. The fact that in the past some of these factors have been adverse to the utilization of aspen stands does not mean that the wood can not be used more widely now and in the future at a reasonable cost and without sacrifice of the quality of the product.

The utilization of the existing stands of aspen has been retarded because the lumber-buying public is not generally familiar with the properties of the wood. There has been little incentive to inform consumers of the properties of a wood which was but little used. There has been a very general tendency to underrate all of the properties of aspen. Other species, such as cottonwood, eastern hemlock, and red gum, have passed through a similar stage. A comparison of the properties of aspen with those of other well-known woods will correct some of the existing erroneous ideas and should aid in the better utilization of the species.

The other woods with which aspen is compared are those that are used for many of the same purposes. In addition, comparison is made with a few of the best known species of the Lake States. The comparisons are made in Table IX by using aspen as 100 points. The other woods are shown as so many points above or below aspen.

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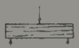
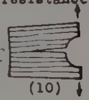
[2] This section under the general heading "Properties," that deals with the mechanical properties and characteristics of the wood and the grading of the lumber, was written by R. P. A. Johnson, engineer, Forest Products Laboratory, Madison, Wisconsin.

TABLE IX

AVERAGE MECHANICAL AND PHYSICAL PROPERTIES OF CLEAR WOOD OF ASPEN COMPARED WITH OTHER SPECIES*

Species	Weight per cubic foot		Shrinkage	Bending strength	Compressive strength (endwise)	Stiffness	Hardness	Shock resistance	Nail-holding power	Splitting resistance
	Green (1)	At 12 per cent moisture content (2)	(3)	 (4)	(5)	(6)	(7)	(8)	(9)	 (10)
	Pounds	Pounds	Points	Points	Points	Points	Points	Points	Points	Points
Aspen†	43	27	100	100	100	100	100	100	100	100
Largetooth aspen†	43	27	105	105	119	121	123	94	105	131
Basswood	41	26	142	97	107	118	100	81	101	118
Eastern cottonwood†	49	28	124	98	110	115	116	109	99	169
Balsam poplar†	40	23	94	76	83	89	81	64	–	96
Yellow poplar	38	28	107	113	117	126	129	87	112	171
Northern white cedar	28	22	62	79	90	73	97	70	80	93
Balsam fir	45	26	93	94	116	110	100	75	–	76
Eastern hemlock	50	28	88	114	136	113	165	100	117	88
Jack pine	50	30	92	102	126	104	155	116	129	127
Northern white pine	36	25	75	100	116	111	113	82	114	98
Eastern spruce‡ (commercial)	34	28	113	111	129	121	126	101	113	100

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* This table is for use in comparing the clear wood of aspen with that of other species, or for comparing aspen lumber with lumber of other species containing like defects.

† Sometimes sold mixed with aspen under the commercial name of popple.

‡ Average red and white spruce.

Physical Properties

Structure, color, and odor of aspen wood.—Aspen has an exceedingly fine and uniform texture. The pores are not visible to the unaided eye on smooth-cut end surfaces and the annual growth rings are visible only upon close inspection. The result is a wood of uniform surface with practically no distinct markings. Finshed, it has a silky luster.

The wood resembles that of large-tooth aspen so closely, both in general appearance and cellular structure, that they can not be distinguished from one another. In structure, it also closely resembles that of various species of cottonwood. It can, however, usually be distinguished from them by the larger pores of the cottonwood, which are visible to the eye on a smooth-cut end surface.

As a rule the wood of aspen, both heartwood and sapwood, is practically white. On exposure to light and air the surface becomes a pale brown or pinkish brown. The inner part of aspen logs is frequently discolored by decay. In the early stages of decay, the infected part may be mistaken for heartwood. The wood around the knots is also colored brown, which contrasts strongly with the white wood and, at a casual glance, makes the knots appear much larger than they are (Fig. 6). The source of the dark color is unknown. It has been ascribed to action of wood-destroying fungi. Microscopical examination of some of the dark colored wood, however, failed to reveal any sign of fungous action.

The cottonwoods, balsam poplar, and basswood are other light-colored woods with which aspen is occasionally confused. The cottonwoods and balsam poplar, however, have a pale gray or grayish brown heartwood, whereas that of aspen is white. Basswood is distinguished from aspen by the finer structural differences rather than by color. Aspen lumber when surfaced, however, has a characteristic silky lustre that is more pronounced than in any of the foregoing woods.

There exists a decided preference for light-colored or white woods for a number of uses; the reasons for which are sometimes difficult to understand, as in the case with matches and ladders. If markings and stencils are to be used, the whiteness has a utility value. Other users prefer white wood because of appearance. Butter boxes and comb-honey containers are uses in which the clean appearance of a white wood is desirable.

Aspen has only a slight odor, like that in the cottonwoods and balsam poplar, noticeable in shops when the wood is worked. Because the wood has little if any tendency to impart odor to foodstuffs, it is used for butter boxes, egg crates, and excelsior. The odor of basswood, tho not strong, is distinctly different from that of aspen and helps in distinguishing the two woods.

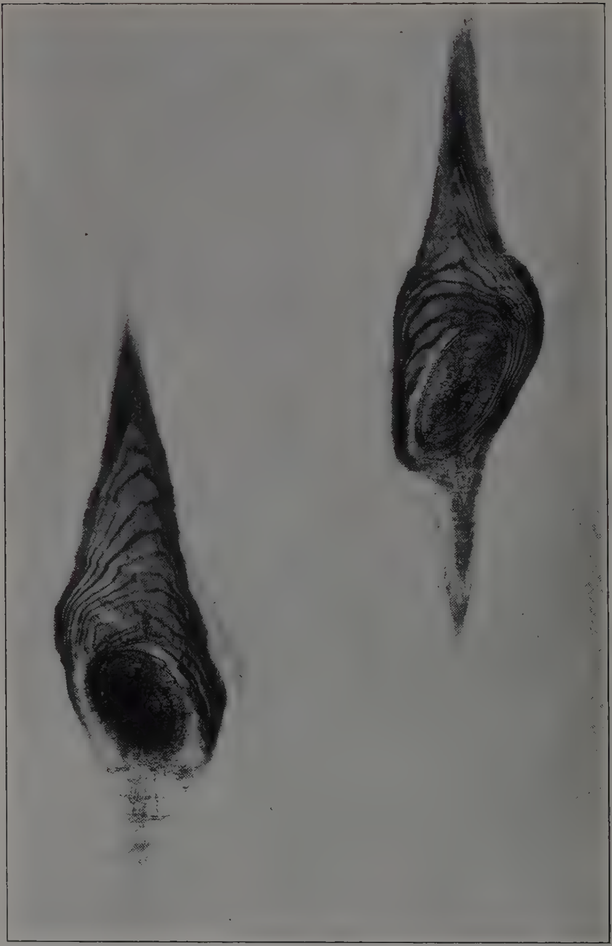

Fig. 6. The Knots in Aspen Are Characteristic of the Species. No Trace of Decay Was Found in Microscopical Examinations of the Dark-colored Wood Surrounding the Knots

Weight per cubic foot (green and air-dry).—Aspen is one of the hardwoods of light weight. In a thoroly air-dry condition (12 per cent moisture content in the Lake States) aspen weighs on the average, 27 pounds per cubic foot. One thousand board feet of nominal 1-inch dry aspen lumber surfaced to a thickness of 25/32 inch would weigh about 1,760 pounds. Similar amounts of other woods would weigh: basswood about 1,690 pounds, eastern cottonwood 1,830 pounds, sugar (hard) maple, about 2,870 pounds. A comparison of the weight of air-dry aspen with other species, all valued for their lightness, is shown in Figure 7.

Generally the lighter the weight of the dry wood the weaker and softer it is. Like all general rules, this one has some exceptions. Thus, altho yellow poplar is heavier and harder than aspen, aspen is higher in shock resistance. Large-tooth aspen and aspen weigh the same, but large-tooth aspen is harder and tests higher in all strength properties except shock resistance or toughness (Table IX). Such exceptions usually occur where differences in weight are small. Where differences in weight are large, as between maple and aspen, the general rule holds true.

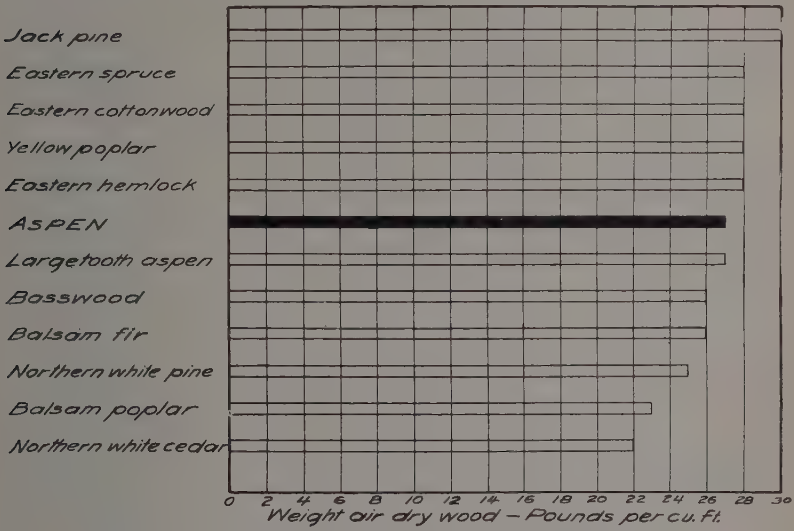

Fig. 7. Weight of Air-dry Aspen, 12 per Cent Moisture Content, Compared with the Weight of Several Other Species

The light weight of aspen is obviously an asset or a liability, depending upon the use to which the wood is put. Lightness is an asset in boxes, pails, and other containers because it reduces the cost of transportation. Likewise, wood of light weight is preferred for spools and for excelsior. Ladders made of lightweight wood are easier to handle than those made of heavy woods. Woods of light weight are also preferred for toys for small children. The tare or dead weight of vehicle body parts may be lessened by the use of lightweight woods. For flooring, stringers, butcher blocks, and similar uses, woods that are heavier and harder than aspen are preferred. Aspen is best adapted to uses where lightness is more important than strength and where a combination of strength and lightness is desired.

Shrinking and swelling.—Small shrinkage is one of the favorable properties of aspen. Changes of dimension with changes in atmospheric conditions are the source of many troubles encountered in the use of wood. The objections to changes in size of interior trim, doors, windows, staves, and ready-cut stock are well known.

The shrinkage and swelling of aspen with moisture changes is less than that of basswood, eastern cottonwood, or yellow poplar, woods favored by manufacturers of articles with small srinkage requirements. Northern white pine and northern white cedar, woods widely known for their small amount of shrinkage, shrink less than aspen. The difference between these species and aspen, however, is less than the difference between aspen and basswood.

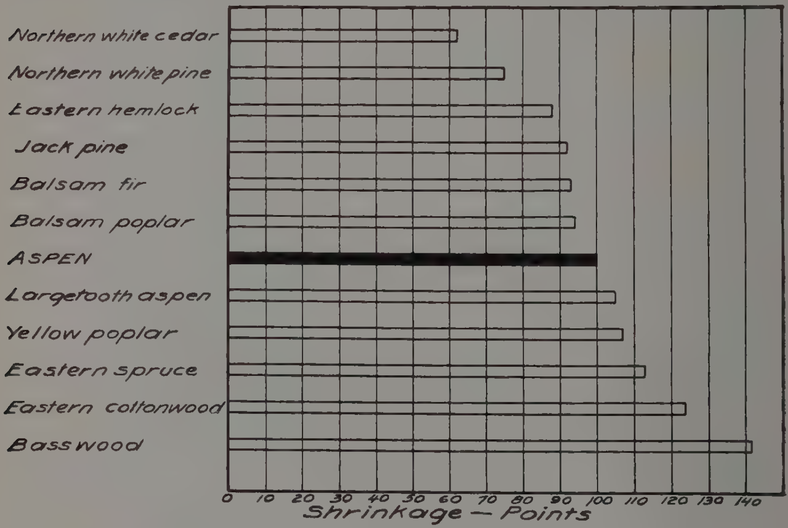

Fig. 8. Comparison of the Average Shrinkage of Aspen with Several Other Species

Aspen has a low shrinkage and consequently will not expand or contract much with slight changes in moisture content.

Comparisons of the shrinkage of aspen with that of several other species are shown in Figure 8, which is based on the total shrinkage from a green to an oven-dry condition. The relative change in dimension that may be expected with different species in service with any given change in atmospheric or moisture conditions may be observed in Figure 8.

Trouble from changing dimension in service is more often caused by the use of green or insufficiently dried lumber than to the inherently high shrinkage of the species. Any advantage which aspen may have as a result of its low shrinkage may be more than lost by the use of wet lumber. The difference in the change in dimension in drying from 20 per cent and 12 per cent moisture content to 6 per cent moisture content is greater than the difference in the shrinkage of aspen and any of the species shown in Figure 8. The use of aspen or any other species, therefore, will not insure small change in dimension unless the wood is dried to approximately the average moisture content it will have in use.

Mechanical (Strength) Properties of Wood

Bending strength.—The clear wood of aspen has the same bending strength as northern white pine (Fig. 9). Northern white pine has been used for years in construction work where bending strength is important. The clear wood of eastern spruce and eastern hemlock, two species also used largely in construction, is slightly higher in bending strength than that of aspen. The bending strength of construction lumber is dependent more upon the defects present than upon the strength of the clear wood. This along with other factors means that aspen has better prospects for industrial and fabricated uses requiring small, clear pieces than for construction uses. Brush and broom handles, toys, matches, kitchen utensils, and washboards are examples of industrial uses requiring small, clear pieces. Altho properties other than bending strength are usually of major

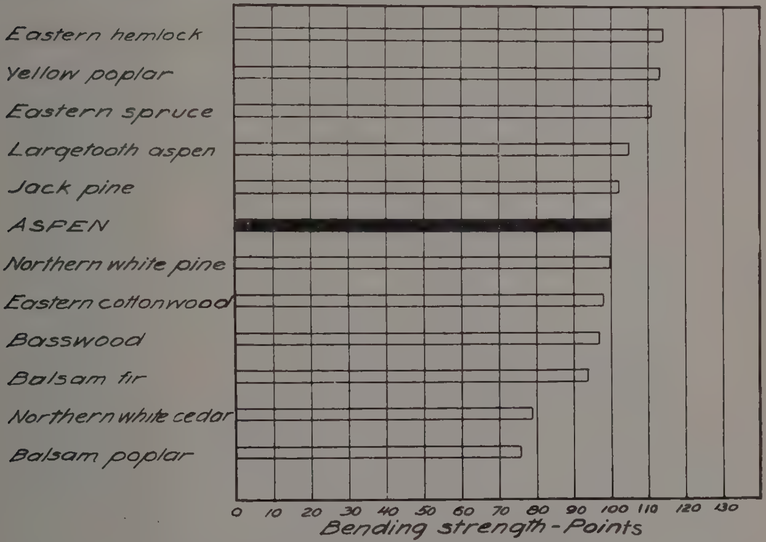

Fig. 9. Average Bending Strength of the Clear Wood of Aspen Compared with Several Other Species

The bending strength of aspen compares favorably with that of a number of important commercial species. The strength of large-sized stringers, heavy joists, and rafters depends primarily on the size, number, and location of knots and other defects.

importance in such uses, some bending strength is necessary for satisfactory service.

The use of aspen where bending strength is of first importance probably will always be limited. Aspen lumber is not generally available in the sizes and grades desired for construction work. Small amounts for construction are sometimes used locally, but the largest use of aspen timber for construction purposes is in round form for mine timbers. Even as mine timbers, the use of aspen is confined almost entirely to mines close to aspen stands. Where mine timbers must be shipped in, heavier, stronger, and more decay-resistant woods are preferred.

Compressive strength (endwise).—Aspen is used in only a few cases where high compressive strength (endwise) is desired. Compressive strength (endwise) is an important requirement of posts and short columns that are required to support heavy loads. Such structural members are usually 6 by 6 inches in cross section or larger. Practically no material of this character is produced from aspen because of the small size of the tree.

Considerable aspen is, however, used for mine timbers where compressive strength (endwise) is an important requirement. For mine timbers it is used mostly in log form. Occasionally pieces 2 by 2

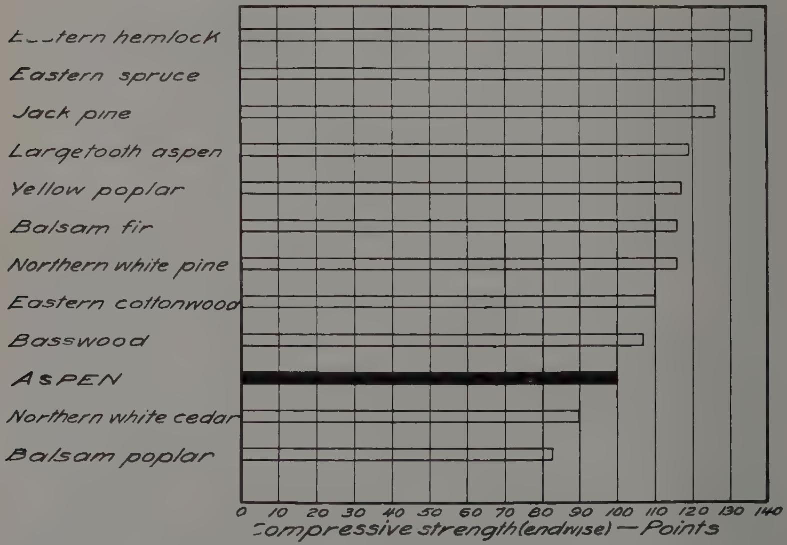

Fig. 10. Average Compressive Strength (endwise) of the Clear Wood of Aspen Compared with Several Other Species

Aspen posts and short columns have low load-carrying capacity. The strength of large-sized posts depends mostly on the size, number, and location of knots and other defects.

inches or less in cross section and 20 inches or shorter in length are required to support a heavy load. Such posts, to have an equal load-carrying capacity, should be slightly larger than cottonwood or jack pine posts, but may be somewhat smaller than balsam poplar or northern white pine (Fig. 10). Mixed lots of posts, sold as "popple," "poplar," or "cottonwood," average higher in strength than straight lots of aspen posts. This is because of the higher compressive strength (endwise) of cottonwood and large-tooth aspen.

The compressive strength of aspen is comparatively low. However, it is generally sufficient for most of the uses into which the species goes, inasmuch as in these uses properties other than compressive strength usually control.

Shock-resisting ability.—Aspen is relatively shock resistant for a lightweight wood. Basswood, yellow poplar, and northern white pine, woods noted for their softness and light weight, are lower in shock-resisting ability than aspen (Fig. 11).

Shock-resisting ability, or toughness, is dependent on the dry weight of a wood; therefore, the slightly heavier cottonwood and jack pine are somewhat more shock resistant than aspen. Very heavy hardwoods, such as ash and elm, are much higher in this property than aspen.

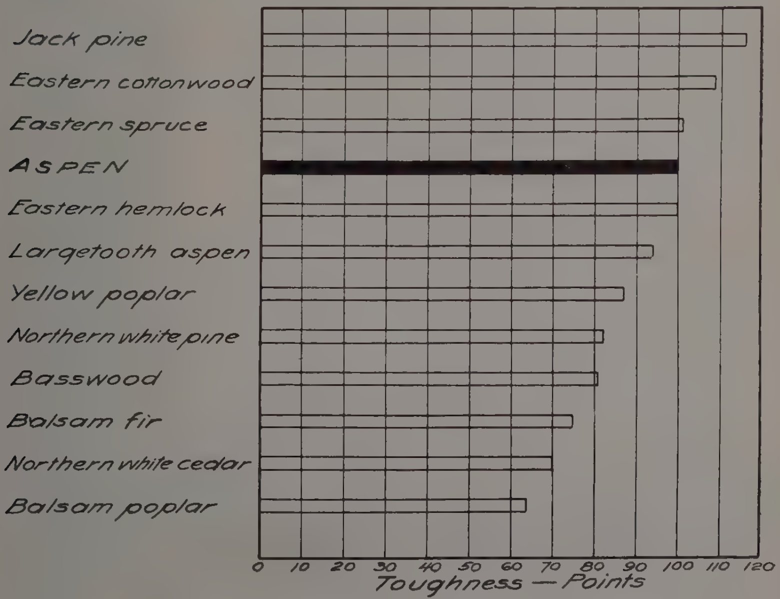

Fig. 11. A Comparison of the Average Shock-Resisting Ability or Toughness of the Clear Wood of Aspen with Several Other Species

The shock-resisting ability of aspen contributes to its successful use as canoe frames, matches, excelsior, toys, and crating.

The shock resistance possessed by aspen increases its range of usefulness. It is an asset in crating, consequently much aspen is used for this purpose, particularly in the form of barky strips. Basket hoops, canoe frames, and ladders are examples of other uses employing lightweight soft woods, where shock resistance is also a desired property. Even for small articles, such as golf tees, matches, and parts of toys, shock-resistance is an advantage. In mine timbers, either round or sawed, shock resistance is desired because tough woods give more warning of failure than brittle woods. The well-known qualities of aspen excelsior is largely due to the toughness of the wood combined with other properties desired for this material. In general, while the shock-resisting ability and other properties of aspen are not sufficient to meet the requirements for such uses as ax handles, pitchfork handles, baseball bats, and hockey sticks, they are sufficient to meet the requirements for the uses to which lightweight softwoods are usually put.

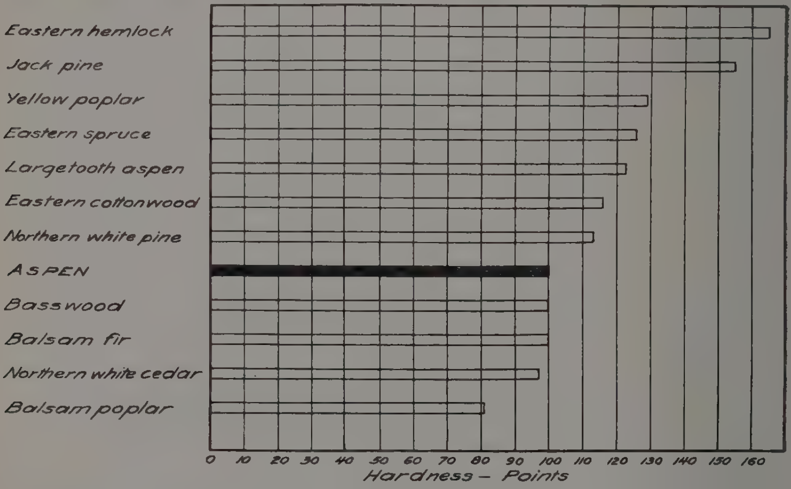

Fig. 12. Average Hardness of Aspen Compared with Several Other Species

Aspen is a soft hardwood. It is suitable for uses where softness rather than hardness is desired.

Hardness (or softness).—A number of woods such as aspen, northern white pine, basswood, and yellow poplar, are in demand, largely, because of their softness. Aspen, basswood, and balsam fir have about the same average softness. They are softer than northern white pine and yellow poplar (Fig. 12).

The greatest advantage of the softness of aspen is in the working of the wood. Wood for excelsior, matches, baskets, dowels, veneers, and spools must be easy to cut or shape. For some uses, such as drawing and drafting boards, softness is desired. Aspen is adapted to uses where softness is desired either in manufacture or in service.

Aspen is soft and uniform in texture, i.e., it does not have alternate bands of hard and soft wood. Such woods are easier to work than those with non-uniform texture. In this respect aspen is very similar to basswood and yellow poplar, which are preferred for a number of uses because of their softness and uniform texture. Aspen can meet requirements for a combination of uniformity of texture and softness equally as well as either yellow poplar or basswood.

Stiffness.—Aspen is not a stiff wood. It will bend more under a given load, other things being equal, than jack pine, basswood, or northern white pine, but less than balsam poplar or northern white cedar. The stiffness of aspen is compared with that of a number of other species in Figure 13. The comparisons are for clear wood but apply almost as well to wood containing knots or other defects, for defects have little if any influence on stiffness.

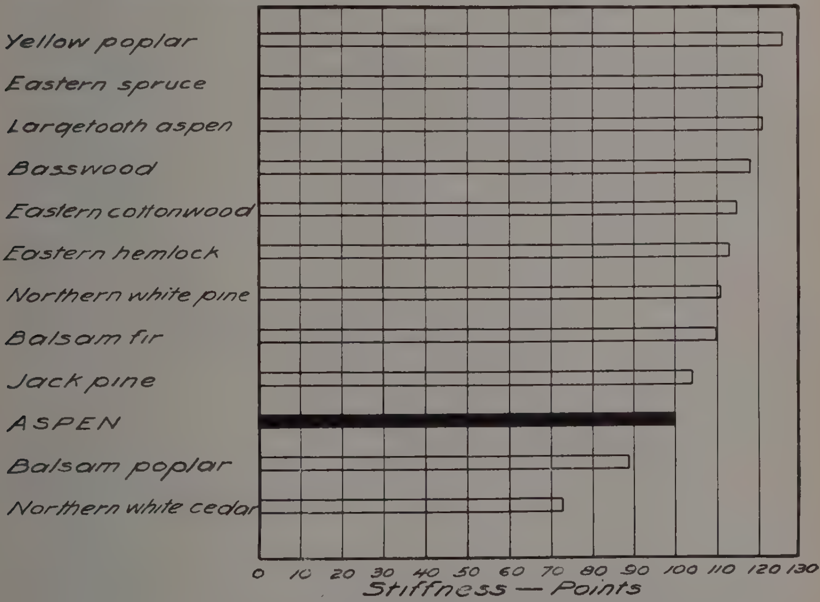

Fig. 13. A Comparison of the Average Stiffness of the Clear Wood of Aspen with Several Other Species

Aspen is not a stiff wood, but oversizes are not necessary to obtain sufficient stiffness to meet the requirements of most of the uses into which the wood goes.

Stiffness is one of the important requirements of joists, studs, and other framing material. Aspen framing material would have to be somewhat larger in size than that of eastern spruce or eastern hemlock to have equal stiffness. Aspen is used for framing only in small quantities, as it is not available in as many sizes and grades as a number of the coniferous woods.

In most of the uses to which aspen is put, stiffness is not of importance. The stiffness of aspen is such that oversizes are not necessary to obtain sufficient stiffness for such uses as baskets, boxes, small handles, and beekeepers' supplies.

Nail-holding power.—The average holding power of a 7-penny cement-coated nail driven 1¼ inches into the side grain of dry aspen is 194 pounds.[8] The same sized nail driven into green aspen would have about the same holding power when first driven. The holding power would, however, decrease rapidly as the wood dried (Fig. 15). The holding power of the nails driven into green aspen is only about 20 pounds after the wood has thoroly dried.

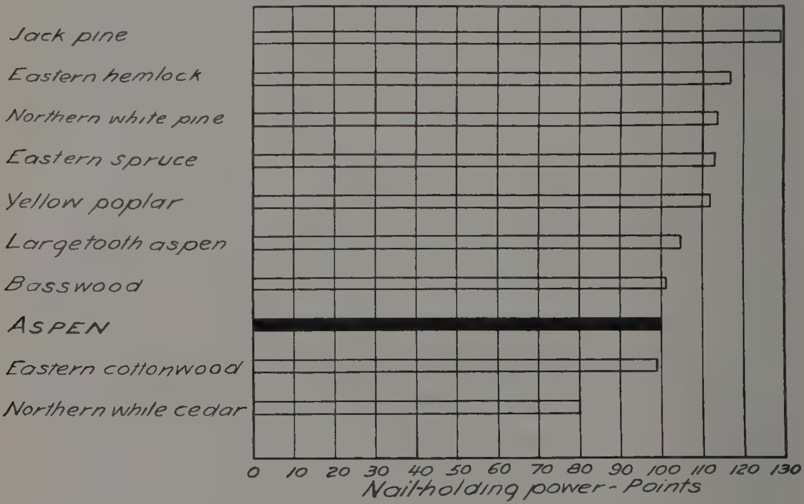

Fig. 14. The Nail-holding Power of Aspen Compared with That of Several Other Species

Aspen has about the same nail-holding power as some of the soft hardwoods of light weight, but it has somewhat less nail-holding power than white pine. In service, the small tendency of aspen to split in nailing results in little loss in holding power from this cause.

The nail-holding power of aspen is comparatively low, about the same as that of basswood and eastern cottonwood. Jack pine, eastern hemlock, and northern white pine have a higher nail-holding power than aspen (Fig. 14). More or larger nails must, therefore, be used with aspen to obtain a nail-holding power equal to that of the latter woods, provided they split no more than aspen in nailing. Fortunately the softness and uniform texture of aspen usually permits the use of a nail large enough to obtain the necessary nail-holding power without undue hazard from splitting. For uses, such as framing, where nail-holding power is desired to hold a covering, an increase in the size or number of nails is not generally necessary to obtain satisfactory nail-holding power. Even in standard food boxes where the nailed joints are usually the weakest parts, recent tests at the Forest Products Laboratory showed that it was not necessary to increase the size or number of nails in aspen boxes to obtain satisfactory resistance to rough handling.[4] The aspen boxes stood more rough handling than boxes of a number of species with higher nail-holding power. The smaller tendency of aspen to split at the nails was apparently sufficient to more than compensate for its lower nail-holding power.

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[8] "Nail-holding Power of Various Species of Wood," by L. J. Markwardt and J. M. Gahagan, Forest Products Laboratory, published in "The Timberman," August, 1929; the "Southern Lumberman" of July 15, 1929, contains detailed data on nail-holding power of 50 species including aspen.

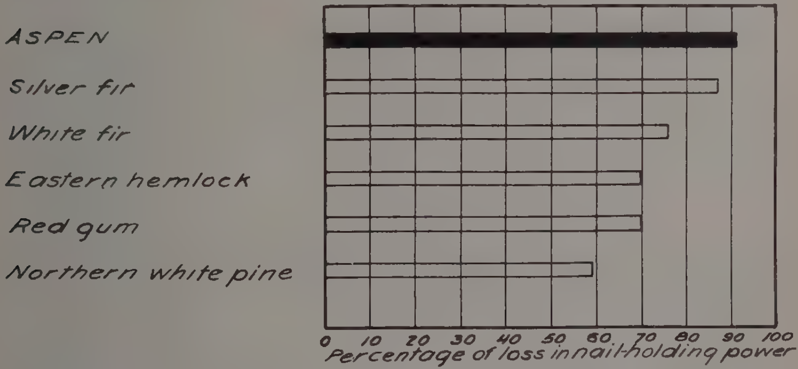

Fig. 15. The Loss of Nail-holding Power of Aspen and Several Other Woods When Nails Are Driven Into Green Wood and Pulled After Seasoning

So large is the loss in nail-holding power under these conditions, that it is poor practice to nail into the green wood of any species which will later dry in service.

Nails driven into green aspen lose about 90 per cent of their nail-holding power when the wood has thoroly dried (Fig. 15). Satisfactory service can not be expected when nails are driven into green aspen and the wood allowed to dry out later in service. It is poor practice to nail any species while in a green condition, but especially so with aspen.

Splitting.—Aspen is straight grained and consequently easy to split. In this respect it is about the same as eastern spruce. Eastern cottonwood and yellow poplar are much harder to split than aspen; balsam fir and eastern hemlock are somewhat easier (Fig. 16).

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[4] Results of these tests on boxes made of aspen and eight other woods are given in articles by T. A. Carlson, published in "Packages," 32, No. 3: 11, 14, 16, 22; March, 1929; "Packing and Shipping," 55, No. 12: 21-25, March, 1929; and "Mississippi Valley Lumberman," 60, No. 11: 26-27, March 15, 1929.

Some uses require a wood that is easy to split and others, a wood that is hard to split. Matches, toothpicks, and shoe pegs are uses that require easily split woods; uses such as vehicle body parts, where bolts are used for fastenings, require wood with high splitting resistance. Aspen is better suited to the first than to the second type of uses.

Splitting in nailing is dependent more upon the softness and texture of wood than upon the splitting resistance. The softness and uniform texture of aspen are responsible for it splitting less in nailing than many harder woods with higher splitting resistance. Washboards, brooms, and boxes require woods with little tendency to split in nailing. Aspen is well adapted to such uses because its low splitting resistance is more than offset by its softness and texture, resulting in a low tendency to split in nailing. The tendency of small or thin parts, such as egg case tops, sides, or bottoms, to split in nailing can be materially reduced by the use of blunt-pointed nails, but at some sacrifice in holding power. Aspen veneer or thin shooks can often be successfully nailed with blunt-pointed nails when it is impractical to reduce splitting sufficiently by reducing the size of the nail.

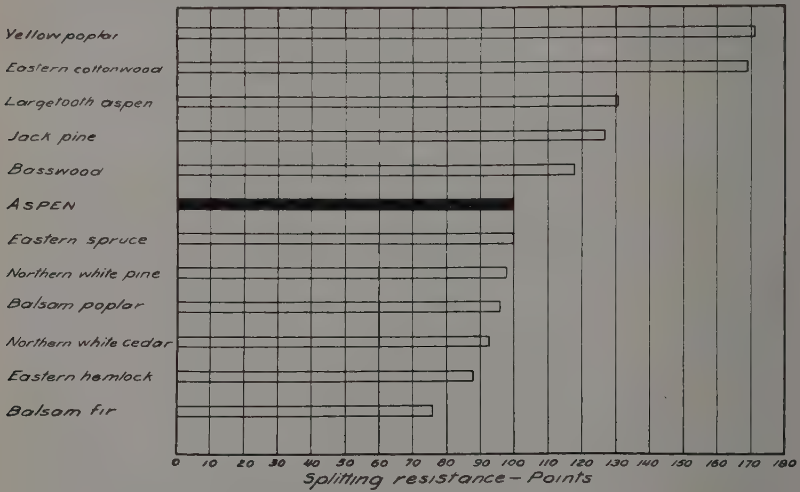

Fig. 16. Comparison of the Splitting Resistance of the Clear Wood of Aspen with That of Several Other Species

Splitting resistance is a measure of the resistance to splitting from the action of wedges and bolts but it is not a measure of the tendency to split in nailing, which is dependent largely on the hardness and texture of the wood.

Decay Resistance

Aspen is classed with basswood, cottonwood, and the true firs in the matter of decay resistance. The heartwood of these species is low in decay resistance. The sapwood of all species has a low resistance to decay.

When the heartwood or sapwood of aspen is to be used for railway ties, poles, fence posts, mine timbers, or other uses where it is in contact with the ground or exposed to moist or wet conditions, it should be treated with a preservative. Furniture, brush handles, boxes, and similar articles are seldom used under conditions favorable to decay. In such uses, decay resistance is of no importance and untreated aspen will last as long as the decay-resistant woods.

The actual life of untreated aspen in contact with the ground varies widely. The life of aspen fence posts, ties, or mine timbers can not be predicted. It depends largely on the conditions under which the wood is used. Untreated aspen fence posts at a high elevation in the southwestern states are still serviceable after 28 years, altho all the aspen posts in a test fence in another location have been removed at the end of 10 years of service, and all but 15 per cent of the posts showed decay. Under favorable conditions, aspen may last only two or three years.

Adaptability to the Manufacture of Pulp and Paper

Aspen can be readily pulped by any of the standard chemical or mechanical processes. It is the standard pulp wood employed in the soda process for the production of certain grades of book papers. However, of the standard processes, the sulphite process probably offers the best prospects for better utilization of aspen in the Lake States. Many mills where such utilization can be made are already established in the Lake States, especially in eastern Wisconsin. These mills have difficulty in obtaining adequate supplies of the species commonly used for pulp and paper. The prospects are that the difficulties will increase with the depletion of the supply of spruce, balsam fir, and eastern hemlock. The large amount of aspen in the Lake States offers a possible solution to the raw material problem of these mills.

Aspen alone or mixed with softwoods is readily pulped by the sulphite process. The adaptability of aspen to pulping by the sulphite process, either alone or mixed with spruce, balsam fir, or eastern hemlock, has been demonstrated by tests made at the Forest Products Laboratory. The yield of pulp per cord of aspen will average about 950 pounds, approximately the same as the yield obtained from eastern hemlock. The unbleached pulp is of excellent color, but usually contains small black specks which disappear on bleaching. The pulp bleaches readily to a high white color. It is not so strong as pulp made from the softwoods[5] but it has other desirable characteristics, such as opacity, bulk, and softness. These properties are responsible for its use in book, tissue, and specialties.

Mills manufacturing sulphite pulp from softwoods can handle aspen satisfactorily with their regular equipment. About the only change that needs to be made in processing the pulp is the use of a set of smaller cut screen plates. Information on how to treat or process aspen pulp or mixed aspen and softwoods can be obtained from the Forest Products Laboratory at Madison, Wisconsin.

The sulphate and soda processes produce an easily bleached aspen pulp and give yields of from 45 to 50 per cent. These processes, however, are applicable to practically all North American hardwoods and in addition can be used with cornstalks and other materials.

Mills producing soda pulp are located largely outside of the Lake States. The available supply of raw material is much greater than in the case of sulphite mills, and the demand for soda pulp or sulphate pulp of an equivalent grade, shows little tendency to increase. The soda and sulphate processes, therefore, do not offer promising prospects for the utilization of the aspen stands.

The ground-wood process was first employed with aspen. For a long time it was not considered suitable for other woods. Spruce, however, has largely supplanted aspen in the production of ground-wood pulp because it requires less power for grinding and, in addition, gives a pulp of greater strength and better felting properties. Aspen ground-wood pulp is light colored and about 85 per cent of standard strength. Some aspen is now ground for use in newsprint paper and in boards. The complete substitution of aspen ground-wood pulp for spruce ground-wood pulp in newsprint would require an increase in the amount of chemical pulp to compensate for the lower strength properties.

Characteristics Depending on Combinations of Properties

Seasoning characteristics.—Manufacturers are experiencing no difficulty in air-drying aspen. The wood has shown no tendency to surface check or warp excessively, nor has it exhibited any other serious seasoning troubles.

The literature on aspen and the lumber trade in general ascribe to it a tendency to warp. The small amount of information available does not reveal the cause of this general opinion. A number of one-inch boards and resawed inch stock were dried at the Forest Products Laboratory to about 12 per cent moisture content. The thin resawed stock furnished a severe test of warping tendencies. A careful inspection of the specimens showed that the thin, as well as the thicker, specimens held their shape well. Only one specimen showed pronounced warp. Inspection of a shipment of rough 4/4 air-dried stock at about 16 per cent moisture content showed little warping; in fact, no more than would be expected of any of the principal commercial hardwoods. In a test made at the Forest Products Laboratory of the kiln-drying of aspen dimension stock 1 by 1 inch and also 3 by 3 inches in cross section, and 48 inches long, the stock was dried without developing any pronounced defects, such as collapse, honeycombing, excessive surface checking, or warping. The blanks remained sufficiently straight for furniture stock and the warping was less than that shown by the red gum and yellow birch blanks, which were also tested.[6] Thus the general opinion that aspen has a pronounced tendency to warp may have resulted from lack of care in seasoning; from a comparison with white pine, which is one of the best of our native species for holding its shape; or it may have developed from observing the pronounced warping sometimes observed in boards cut from small, rapid growing trees.

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[5] The strength properties of unbleached aspen pulp and of pulp made of a mixture of one-half aspen and one-half white spruce and a mixture of one-half aspen and one-half eastern hemlock are shown in detail in an article entitled, "Pulping of Hardwoods and Mixtures of Hardwoods and Conifers by the Sulphite Process," by William H. Monsson, Forest Products Laboratory, published in Paper Trade Journal, April 26, 1928.

No extensive research has been conducted at the Forest Products Laboratory to determine the most efficient methods of air- or kiln-drying aspen. Experience with other species, such as the gums, however, indicates that aspen can be successfully dried by modern methods.

Until more adequate data are available the kiln schedules recommended for drying birch[7] can be used for drying aspen. The kiln schedule of the Forest Products Laboratory for birch of 6/4 inch thickness or thinner recommends temperatures from 140 degrees initial to 170 degrees F. final, and relative humidities from 80 per cent initial to 20 per cent final. Such a schedule is safe for aspen in so far as preventing honeycombing, collapse, and excessive checking.

Ability to stay in place.—Ability to maintain size and shape is a desirable property in practically all uses into which aspen goes. Tho not the most important, it is probably the most generally desired of the properties. Tendency to change size or shape increases the difficulty of construction and fabrication, injures appearance, and adversely affects service. The desirability of retaining size and shape in such uses as hosiery boards, furniture, doors, fixtures, shoe lasts, sashes, woodenware, dimension stock, and forms is well known. Siding and sheathing that fail to stay in place not only cause leakage in walls but also mar the finished appearance of the structure.

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[6] The results of the tests are presented in a report, "Kiln Drying of Small Dimension Stock," by R. H. Grabow, Forest Products Laboratory, Madison, Wisconsin.

[7] For schedules on drying birch see "Kiln Drying Handbook," Department of Agriculture Bulletin No. 1136, p. 49.

The ability of aspen to stay in place depends upon a combination of its shrinkage and tendency to warp. Shrinkage causes a change in dimension; warping results in a change in shape. The smaller these changes, the better the wood stays in place.

A comparison of the tendency of aspen and several other woods to change dimension with changes in moisture conditions is shown by the shrinkage comparison in Figure 8. The unequal shrinkage of heartwood and sapwood, the abnormal shrinkage of compression wood, the presence of knots and cross grain, and the difference in shrinkage of flat grain and edge grain in boards from near the pith cause warping. No satisfactory method of evaluating all these factors for different species has yet been devised. Comparison of the ability of aspen to stay in place with that of other kinds of woods can not, therefore, be made with assurance. Altho a definite comparison can not be made, a conclusion can be drawn from the shrinkage values for aspen and the frequency of occurrence of the other factors that cause warping.

Aspen has a low shrinkage comparing favorably with many of the hardwoods. It is straight grained, being similar in this respect to basswood and yellow poplar. Only an occasional board of aspen contains both heartwood and sapwood and consequently there is practically no warping due to unequal shrinkage of heartwood and sapwood. Abnormal compression wood has seldom been observed and is responsible for little if any warping in aspen. The occurrence of knots is largely a matter of grade. For the same grade knots will probably cause no more warping in aspen than in other woods. In the mill run of aspen, knots cause somewhat more warping than they do in basswood or cottonwood because the small size of the aspen tree results in a larger number of boards from near the pith than is obtained from species with larger diameters. Thus it appears that aspen should stay in place well when compared with other hardwoods. The small number of tests made at the Forest Products Laboratory on aspen and the experience of at least one consumer confirm this observation. However, additional service records and experimental data are necessary to determine more definitely the ability of aspen to stay in place.

Gluing characteristics.—Glued joints that are as strong as the wood itself are easily obtained with aspen (Fig. 17A). Such joints are obtainable with animal, casein, or vegetable glues. Recent tests at the Forest Products Laboratory of joints made with these glues resulted in an average joint strength of 1,725 pounds per square inch.

Joint failures were either entirely or almost completely in the wood. All of the joints made with casein or vegetable glue showed 100 per cent wood failure. Joints made with animal glue were prepared under good and also under poor gluing conditions. All the joints made under good conditions failed 100 per cent in the wood, and even those that were made under poor conditions failed on an average of 97 per cent in the wood. With all glues and under all conditions of gluing the joints made were as strong as the wood itself.[8] The development of the full strength of aspen with joints made under conditions that in many other woods result in starved joints marks the species as one of the easiest to glue.[9]

Joints made with animal glue under conditions that were more severe than would be employed in a commercial gluing operation, showed only 3 per cent of the failures occurred in the glued joints (Fig. 17B). Moreover, the joints developed an average strength of 1,705 pounds per square inch. Aspen can, therefore, be glued satisfactorily with animal glue under a wide range of conditions. This is an advantage in commercial operations in that it is an insurance against poor joints. In addition, gluing operations do not have to be so carefully watched and controlled to obtain satisfactory results.

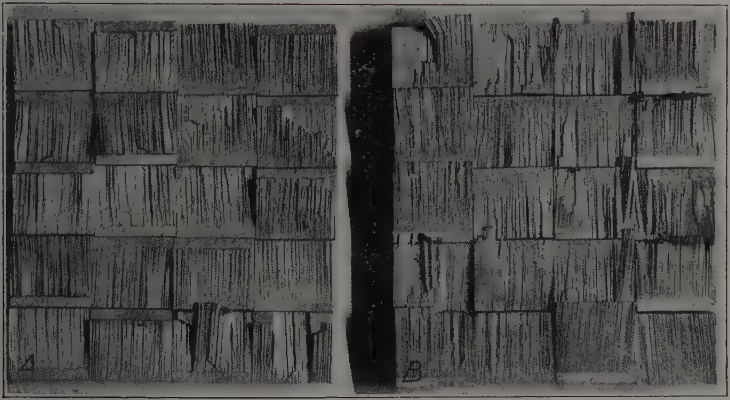

Fig. 17. Characteristic Joint Failures in Aspen Glued with Animal Glue. Even Under Poor Gluing Conditions Most of the Glued Joints Were Stronger Than the Wood

A. Joints glued under good conditions with animal glue. All failures are in the wood. The failures are also typical of those obtained with casein and vegetable glue.

B. Joints glued under poor conditions with animal glue. The smooth surface on some of the specimens shows where the glue rather than the wood failed.

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[8] Gluing schedules A1, C1, and V1, recommended in Tables 7 and 8 of U. S. Dept. of Agr. Bul. No. 1500 for animal, casein, and vegetable glues are satisfactory for the gluing of aspen.

[9] Results of similar gluing tests on 40 other species are shown in U. S. Dept. of Agr. Bul. No. 1500.

The excellent gluing characteristics of aspen adapt it to use for core stock for doors, veneer panels, and similar products. The use of veneers, built-up construction, and other glued-wood products has been steadily increasing for a number of years. The demonstrated excellent gluing characteristics of aspen, therefore, open a number of new markets for it.

Painting and finishing characteristics.—Very little information is available on the painting and finishing characteristics of aspen. A study of the painting characteristics of aspen and a number of hardwoods was started at the Forest Products Laboratory in 1930. It will require two or three years to obtain sufficient data to warrant the drawing of definite conclusions or the making of definite recommendations. Certain general and tentative conclusions can, however, be drawn at this time from data available and general knowledge of the properties and characteristics of the wood.

Aspen is better adapted to paint and enamel than to stain and natural finishes. The uniform texture, light weight, and color indicate that it will take and hold paint well. Good painting characteristics are an important requirement of wood for interior and exterior trim. A few trials made on aspen indicated that the dark streaks which occur in the wood and around the knots can be satisfactorily covered with three coats of white lead paint. No other type of paint has been tried on aspen at the Forest Products Laboratory. A single coat of enamel applied on the three-coat white lead base gave a finish which indicated that aspen can be satisfactorily used for high-class, light-colored enamel work. The wood is reported to take stain well and such figure as the wood has shows up well. Where a pronounced figure is not desired it should prove satisfactory in stain and natural finishes. The wood, therefore, has possibilities for stained and enameled furniture, and for painted or enameled interior trim.

Treating characteristics.—Aspen that has received a good preservative will generally give longer life at lower cost per year than the naturally decay-resistant woods without treatment. Aspen posts that have been pressure-treated with a 25 per cent coal-tar creosote and 75 per cent gas oil mixture have given 13 years service at Madison, Wisconsin, and are still sound.

When pressure-treated material is not available or the cost is too high, the user can do his own treating on the farm, at the mine, or on the job by the hot and cold bath process.[10] It is estimated that under conditions favorable to decay a life of 20 years or more can be expected from aspen posts treated with creosote by the hot and cold bath process. Water-gas-tar or a half and half mixture of waste crank-case oil and creosote applied by the hot and cold bath method will probably give a reasonably long life to aspen, but data are not available on which to base a comparison with the coal tar-creosote treatment.

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[10] The hot and cold bath treatment is described in U. S. Dept. of Agr. Farmers' Bull. No. 744, "The Preservative Treatment of Farm Timbers."

Aspen may also be treated with water solutions, such as zinc chloride and sodium fluoride. These chemicals are best applied by pressure. They may be applied, but with less effective results, by the simple method of soaking well-seasoned wood for a week or more in a tank containing a 5 per cent solution of zinc chloride or a 3½ per cent solution of sodium fluoride. Detailed instructions for preparing solutions and treating by the steeping process may be obtained from the Forest Products Laboratory, Maidson, Wisconsin.

The more effective methods described when applied to aspen make it an economical wood to use under conditions favorable to decay. The life of aspen that has been well treated with preservatives will not differ greatly from that of well-treated material of the more decay-resistant woods. The possibilities of using preservative-treated aspen for many purposes for which the untreated wood is unsuited have been largely overlooked.

Ease of working.—Aspen is an easy wood to work. It is soft and easy to cut, saw, and shape with hand tools. It has a uniform texture and is consequently easy to finish to a smooth surface. Aspen, in both ease of working and character of surface obtainable, is similar to basswood and yellow poplar, both species well and favorably known for their working qualities.

Only easy working woods are suitable for match stock. The use of aspen in the manufacture of matches is a testimonial to the working qualities of the species. Toys, shoe pegs, clothespins, novelties, toothpicks, and woodenware are other products in which aspen is being used because of the ease with which it is worked. Aspen has possibilities in all uses where ease of working, both as to labor and power consumed and character of surface obtainable, is an important or essential requirement.

Altho aspen can be worked with tools that would be impracticable with harder and less uniform textured woods, the use of such tools results in much poorer surfaces. Poor surfaces from dull tools lose for aspen some of the advantages resulting from the smoothness and silky luster of the well-finished wood.

Tho dry aspen dresses to a smooth surface, the wood, when wet, has a tendency to fuzz when dressed. This is a common characteristic of the softer hardwoods, such as aspen, basswood, yellow poplar, and cottonwood, and should be recognized and avoided by proper seasoning before dressing.

Grading of Lumber

Aspen is graded under both hardwood and softwood rules. It is graded as hardwood factory lumber under the rules of the National Hardwood Lumber Association and as softwood yard lumber under the rules of the Northern Pine Manufacturers' Association. Some mills grade the entire output of aspen under the pine rules, whereas at least one large mill grades the upper grades of aspen under the hardwood rules and the lower grades under the softwood rules.

The best utilization of aspen can probably be obtained by using both the hardwood and softwood rules. Most of the industrial uses to which aspen is best adapted require small, clear pieces rather than full-sized boards. The hardwood grades, with the exception of the grade Firsts and Seconds, are cutting grades, and therefore best meet the requirements of such uses. On the other hand, uses, such as crating, boxes, and building items, use common lumber containing knots and other defects. The softwood grading rules are better adapted to the requirements of such uses for they are based on size, quality, and character of the defects.

The following discussion of grades for aspen, therefore, describes the four best hardwood grades: Firsts and Seconds; Selects; No. 1 Common; and No. 2 Common, and also the three lowest softwood grades: No. 3 Common; No. 4 Common; and No. 5 Common. Such a division is purely arbitrary. In practice the demand for the various grades largely determines the grading system applied. Thus, No. 2 Common will probably be graded by hardwood or softwood rules depending upon the nature of the demand for that type of lumber. In fact the companies producing the most aspen are trying out various possibilities with reference to grading and eventually the method followed will probably be determined largely by the type of uses in which aspen finds the most favor.

Under the hardwood rules, aspen grades are identical with those for sap gum, cottonwood, black gum, tupelo, magnolia, and willow. The grades are Firsts and Seconds, Selects, No. 1 Common, No. 2 Common, and No. 3 Common. Sound stain is no defect in any of these grades. They are all standard hardwood grades except No. 2 Common, which requires "sound" instead of "clear face."

The combined grade of Firsts and Seconds in aspen must, under hardwood rules, contain not less than 33 1/3 per cent of Firsts. Figure 18A shows three boards of First and Second grade. The right-hand board is a first and the other two are seconds. Firsts must be 6 inches or more in width and 8 feet or more in length, except that clear pieces 5 inches wide by 10 feet long or longer are admitted. Pieces with 4 to 9 feet surface measure must be clear. Seconds must also be more than 6 inches wide and must be 8 feet long, except that a limited number of clear pieces 5 inches wide and 10 feet long and more are admitted. Aspen is generally cut from small trees and Firsts and Seconds are therefore largely clear stock. The boards are seldom large enough to permit more than one standard defect[11] in Firsts and two standard defects in Seconds.

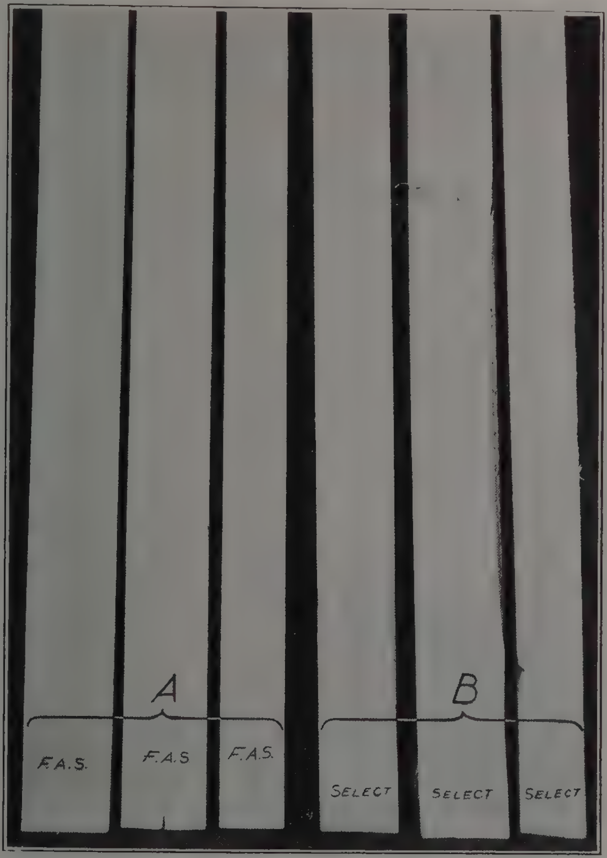

Fig. 18. Firsts and Seconds and Select Aspen as Graded Under Hardwood Grading Rules

A. Firsts and Seconds in aspen are usually clear or contain only one or two defects because of the small size of the boards. The grade is suitable for uses requiring practically clear, full-sized boards.

B. Selects in aspen are suitable for uses requiring large, clear cuttings or for uses that can utilize large cuttings and boards with clear faces but No. 1 Common backs.

Selects must be 4 inches or more in width. Pieces that are 4 to 6 inches wide, however, must be 8 feet long or more and must be practically clear. Pieces 6 inches and more in width and 8 feet and more in length must grade Seconds on the best face and not below No. 1 Common on the poorest face. In addition, the grade also admits boards over 10 feet in length that are not less than 6 inches in width and from which material with a practically clear face and sound No. 1 Common back can be obtained by cutting out defects. Figure 18B shows the type of board commonly found in the grade.

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[11] Standard defects are defined in the National Hardwood Lumber Association Rules, pages 15 and 16, paragraphs 29-33, January, 1930.

No. 1 Common pieces must be 3 or more inches in width and 4 feet or more in length. The permissible amount of material 3 inches in width or less than 8 feet in length in a shipment, however, is limited to a small proportion of the whole. In addition, short pieces 4 to 5 feet and narrow pieces 3 to 4 inches wide and 6 to 7 feet long must be clear. The larger pieces must produce a two-thirds clear face in from 2 to 4 cuttings. The number of cuttings permitted depends on the size of

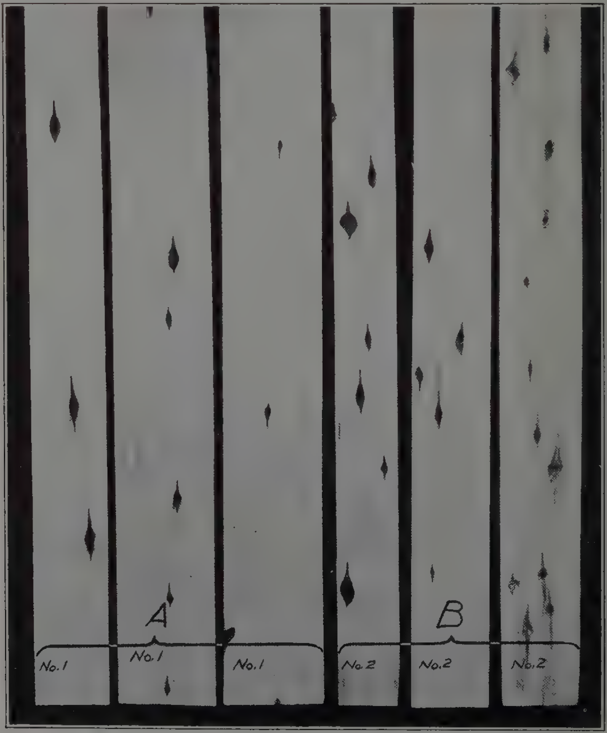

Fig. 19. No. 1 Common and No. 2 Common Aspen As Graded Under Hardwood Grading Rules

A. No. 1 Common aspen boards. The grade is suitable for uses that require some fairly large cuttings but can also utilize a number of small ones.

B. No. 2 Common aspen boards. The grade is suitable for uses requiring only small cuttings.

the pieces. Figure 19A shows the type of boards found in No. 1 Common grade.

No. 2 Common must be 3 or more inches in width and 4 feet or more in length. Lengths under 8 feet are limited to 30 per cent of a shipment. All material must produce 50 per cent clear face in from 3 to 5 cuttings. The number of cuttings permissible depends upon the size of the pieces. Figure 19B shows the type of boards found in No. 2 Common.

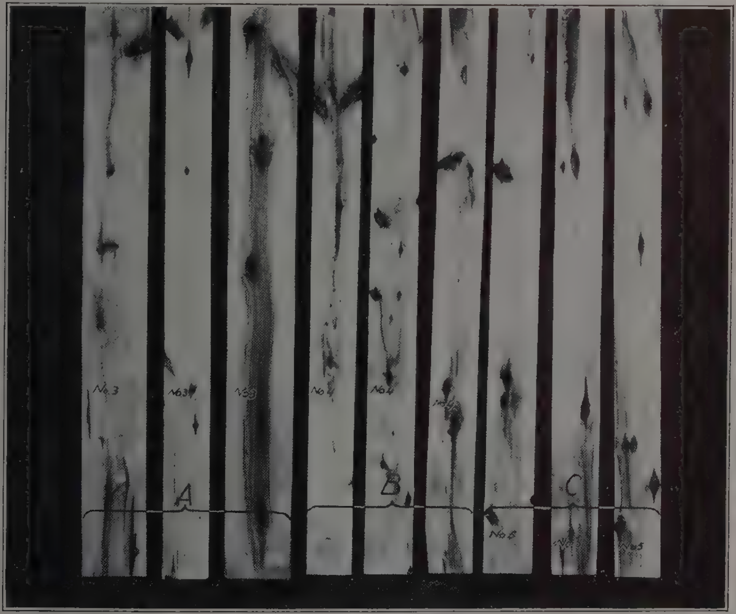

Fig. 20. No. 3, No. 4, and No. 5 Common Aspen Boards as Graded Under Softwood Grading Rules. All Grades Permit Some Waste. The Dark Streaks in the Photographs Are Not Decay and Cause the Grades as Pictured to Appear Poorer Than They Are

A. No. 3 Common. The large coarse-knotted character of the grade is shown. The grade is suitable for rough coverage.

B. No. 4 Common. Low quality lumber admitting the coarsest defects, such as decay and holes. The grade is suitable for crating.

C. No. 5 Common. Must hold together under ordinary handling. The board on the left contains decay which does not show in the photograph. The grade is used largely for rough crating.

Boards of the type commonly found in No. 3 Common, No. 4 Common, and No. 5 Common, as graded under Northern Pine Manufacturers' Association Rules, are shown in Figure 20. Such boards are used as a whole for rough coverage and similar uses or are cut into required sizes for such uses as crating, backing, or lining. No. 3 Common, Figure 20A, illustrates the large, coarse knotted type of stock typical of the grade. Other defects permitted in the grade, such as firm decay, streaks, occasional knot holes, loose and unsound knots, are also shown. About 20 per cent of the run of aspen is No. 3 Common. The No. 3 Common is sometimes combined with the hardwood grade of No. 2 Common and sold as No. 3 and better. The combination "sweetens" the No. 3 grade considerably as may be seen in Figure 19B.

Decay is the predominating defect in aspen No. 4 and No. 5 Common. In addition, large knot holes, wane, and shake are common. No. 4 Common is low quality lumber, generally usable as a whole, but permitting some waste. No. 5 must hold together under ordinary handling and ordinarily require some cutting. About one half of the aspen cut falls into these two grades.

Barky strips is a special grade of aspen used largely for crating. As the name implies a large amount of wane is the outstanding characteristic of the grade. Material of this grade is only suitable for uses that can utilize rough, undressed, comparatively narrow stock containing considerable bark.

In applying the data on properties, careful consideration should be given to the grades. The defects permitted in the grades not only have an important influence on the serviceability of lumber, but may modify the comparisons of properties previously presented. Only a glance is necessary to show that the strength properties of the boards shown in Figure 18 differ materially from those in Figure 20. The comparison of the properties of aspen with those of other species given in this bulletin holds only for the clear wood or between grades having like defects.

Necessity for Further Research on Properties

Information on the properties of aspen is by no means complete. Additional research is necessary to supplement existing data on some properties, such as shrinkage, seasoning, and decay resistance. In addition, there is little information on the painting and finishing characteristics of the species, or on the best method of preservative treatment.

Shrinkage data are needed to enable users to determine the average amount of shrinkage or swelling that takes place with any given change in moisture content. Present data give only the average total shrinkage from a green to an oven-dry condition. Both kiln-drying and air-drying studies are needed to determine the best kiln schedules, methods of piling, and possibilities of decreasing seasoning degrade. Service records on untreated aspen are needed to determine in what uses the decay hazards are too high to permit profitable use of the wood untreated and to determine how well wood stays in place.

There is practically no information on how aspen will take and hold paint when exposed to weather, or on the possibility of using the wood with natural finishes, and only a small amount of information is available on how it will take enamels on interior finishes. Tests now under way at the Forest Products Laboratory will furnish information on the painting characteristics of wood when exposed to weather.

Additional research on properties should aid in the better utilization of the aspen stands of the Lake States. It will permit the species to be used with assurance whereas consumers now hesitate to incur risk of unsatisfactory service. Further research should aid in preventing the use of the species for purposes to which it is unsuited and thus prevent the development of prejudices which tend to retard the use of the species for purposes to which it is suited. Possibly, additional research may point the way to better seasoning methods that will decrease losses between the timber operators and the ultimate consumers and thus make the marketing of aspen more profitable.

UTILIZATION[12]

History of Use of Aspen in the United States

Aspen has long been regarded in the United States as an inferior species. This attitude is due chiefly to the relatively small size of the mature tree and the prevalence of heart rot and decayed knots, rather than to serious deficiencies in the technical or mechanical properties of the wood. It is true that aspen wood lacks unusual strength and any marked natural resistance to decay, but for many uses lack of strength and decay resistance is not, and should not be, considered a limiting factor in its use.

Small sized trees with numerous defects yield only a limited amount of clear lumber. As long as logs of other tree species, larger in size than aspen, were available at a moderate price, little urge existed for utilizing aspen. With a decrease in the availability of basswood, yellow poplar, and several other woods, the possibilities of using aspen wood for certain purposes became apparent.

Altho numerous references are made to the utilization of aspen in literature, practically no complete analysis has ever been made of the situation. In most studies of wood-using industries made by the several states, from time to time, the amount of aspen used is included in the general group "other species." In other estimates of lumber manufacture, aspen is included with cottonwood. The scarcity of any reliable figures on aspen consumption in the past makes it impossible to trace any definite trends in its use.

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[12] This section included under the general heading "Utilization," which deals with the use of aspen wood and lumber, was written by Henry Schmitz, chief of the Division of Forestry, University of Minnesota, St. Paul, Minnesota.

Notwithstanding the fragmentary references to the use of aspen, it is nevertheless apparent that a tremendous change in attitude toward its use has taken place. F. Andrew Michaux in 1859 refers to the wood of aspen as "light, soft, destitute of strength, and of no utility." "These defects," says Michaux, "are not even compensated by an ample size and rapid growth." Michaux was, of course, not only misinformed, but unable to visualize the tremendous number of different uses to which lumber would be put in the future. The very characteristics which Michaux thought were limitations now make aspen preferred for certain uses.

Aspen is utilized to a certain extent almost everywhere it grows, but it is cut in comparatively large amounts only in Minnesota and Wisconsin. Even in these states, the exact cut is unknown, but it is estimated that during 1928 approximately 71,000,000 board feet and 100,000 cords of aspen were cut in Minnesota. No estimate of the total cut of aspen in Wisconsin during the same period is available, but in 1926 at least 33,000 cords of aspen pulp wood, 35,000 cords of excelsior wood, and 4,800,000 board feet of aspen crating lumber were used in that state.

In general, it appears that the consumption of aspen pulp wood will materially increase. It also appears that, owing to certain desirable characteristics, the consumption of aspen dimension and crating stock will greatly increase. Undoubtedly, too, the use of aspen fence posts and mine timbers will increase in the Lake States in the future. The future trend in the consumption of aspen lumber will depend, to some extent at least, on economic considerations.

At the present time, the price of aspen lumber is comparatively low, but as the intrinsic merits of the wood become more fully understood and additional markets are found for it, higher prices will undoubtedly prevail. Aspen saw logs in 1929 sold for from $21 to $22 per thousand feet, board measure, depending on the size and quality. Prices at shipping points were these prices less the freight to the mill.

The Use of Aspen in Europe

It is impossible to draw final conclusions concerning the future use of aspen in America from the use of the European aspen. This is due to the fact that not only is a somewhat different tree dealt with, but also because of the different wood requirements and different economic conditions existing in Europe and America. Nevertheless, a study of the utilization of European aspen may throw some light on the trend which may take place in the use of aspen in America.

Populus tremula is considered a very desirable tree in European countries, particularly Norway, Sweden, and sections of Russia, because of its suitability for the manufacture of safety matches. When and where this market for aspen exists, the tree is favored in silvicultural systems and other tree species are sacrificed for it.

The total amount of wood required by the match industry is not so large as might be expected. Sweden, the largest producer of safety matches in Europe, requires approximately 150,000 cubic meters of match wood, of which almost two thirds is aspen and one third, birch and alder. Thus the annual requirements of aspen by the Swedish match industry is less than 40,000 cords. If aspen of good grade were readily available, it is quite likely that birch and alder would not be used in the manufacture of matches in Sweden. Only the best quality of timber can be used in the production of matches.

In certain sections of Russia where cement is manufactured, European aspen is used for slack cooperage for cement barrels. Wood used for this purpose must be free from large rotten knots. In the United States the cement barrel has all but disappeared, cloth and paper bags having almost entirely taken its place. As in America, aspen is used quite extensively for the manufacture of so-called "wood wool," which is equivalent to our excelsior and used for similar purposes.

Throughout Europe, where aspen occurs naturally, or can be imported at a reasonable figure, many minor uses have been developed for the wood. It is used widely, for example, in the manufacture of boxes, baskets, crates, and berry boxes of various kinds. In England, the wood used for these purposes is imported from northern Russia and in lengths of 7 to 9 feet with diameters of 8 to 16 inches. Aspen is also used in England and on the Continent for dry (slack) cooperage, particularly for food containers. In central Europe and elsewhere, it is used extensively in the manufacture of toys and novelties.

Lumber

That aspen can be used for lumber and that such lumber will give good service under certain conditions have been amply demonstrated. Time alone can tell how successfully it can compete in the market with other woods.

Considerable quantities of aspen have been and are cut into lumber by portable sawmills, particularly in Minnesota. This lumber is used by settlers for practically all ordinary purposes. Unless it has received a preservative treatment, however, it should not be used in contact with the soil or in damp places which are favorable to decay.

Aspen has also been cut commercially for lumber in Minnesota for years and a number of special markets have been developed. Some of the planing mill products are illustrated in Figure 21.

The size of aspen in the Lake States accounts for the small dimensions of aspen lumber products. Products of larger sizes than 2 by 12 inches or 4 by 4 inches are exceptional.

Among the important characteristics of aspen wood that make it suitable for certain purposes are:

1. Combination of strength and light weight
2. Small tendency to split in nailing
3. Excellent gluing characteristics
4. Lack of pronounced odor
5. Combination of softness and uniform texture
6. Complete absence of pitch
7. Light color
8. Ability to withstand sanding without raising grain
9. Suitabality for painting

Much promotional work will undoubtedly be necessary before the market for aspen lumber will be greatly extended. Enterprising producers of aspen lumber are undertaking this work and their efforts will undoubtedly be worth while.

Planking and flooring.—For the last two years, the Minnesota Department of Highways has been experimenting with the use of aspen as an alternate for rock elm and oak, which are ordinarily used for planking longitudinal wearing courses on bridges. The material used is sawed and surfaced to 1 7/8 inches in thickness and from 6 to 12 inches wide. Aspen planking stands up well under the wear and tear of highway traffic. According to the reports received, aspen roughs up and forms a "fur mat" that is quite resistant to wear. When aspen planking in wearing courses in bridges is dented by tractor lugs, the fibers apparently are not cut and they return to their normal position in a short time. Similar treatment cuts the fibers of harder woods, such as elm or oak, and the planking deteriorates rapidly under continued abuse.

Aspen planking used for this purpose, or for any other where decay conditions are favorable, must be treated with suitable wood preservative. The Minnesota Highway Department now gives bridge planking an empty cell treatment with coal-tar creosote with a final retention of six pounds per cubic foot. Aspen planking has long been used for barn floors because of its resistance to mechanical wear.

Some softwoods of light color and uniform texture have recently been used successfully for floors in dwellings, gymnasiums, and armories. Aspen, however, is softer and lighter-colored than any of the woods so far used. It may dent and mar too easily to be satisfactory or its light color may not prove popular. A few installations are necessary to determine whether aspen is a desirable wood for high-class flooring. It is possible that factory floors of aspen wood blocks might prove successful. Blocks used for this purpose are ordinarily treated with a wood preservative to render satisfactory service; aspen should be no exception to this practice.

Interior trim and finish.—Probably one of the most promising fields for aspen lumber is interior trim and finish. Its small tendency to split in nailing, lack of resin, reaction to sanding, and suitability for painting comply with most of the requirements for interior trim or finish, especially when it is to be painted or enameled. Aspen wood shrinks no more than other woods commonly used for this purpose and less than others. Items of interior trim now manufactured from aspen are shown in Figure 21.

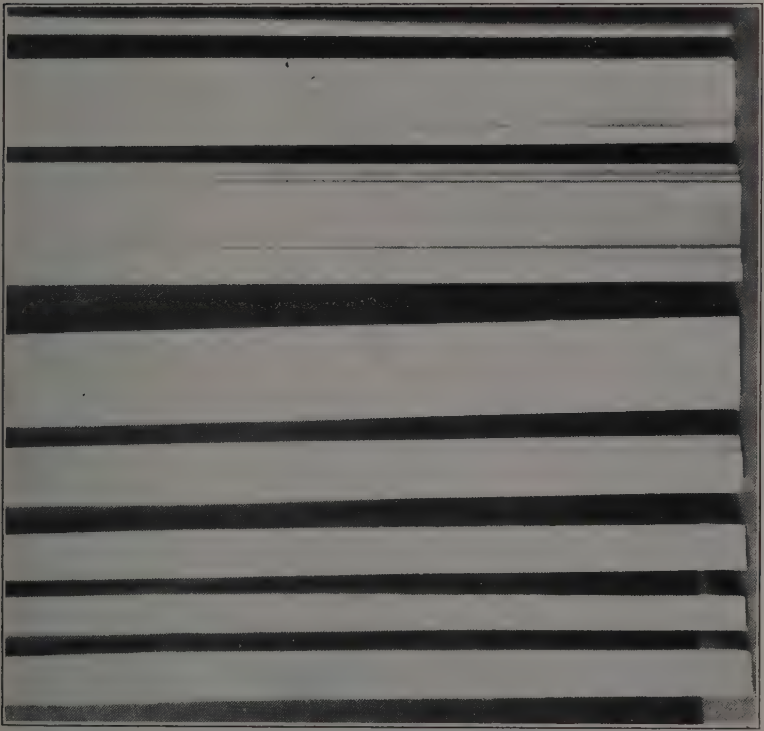

Fig. 21. Types of Aspen Molding Stock

Exterior trim.—Woods very similar to aspen in properties and characteristics have been used extensively in the past for exterior trim. Basswood and yellow poplar siding, cornice, and trim are found on a number of old houses. The demand for these woods for special and more exacting uses has very largely removed them from the exterior trim market. Aspen will probably have a somewhat similar develop-

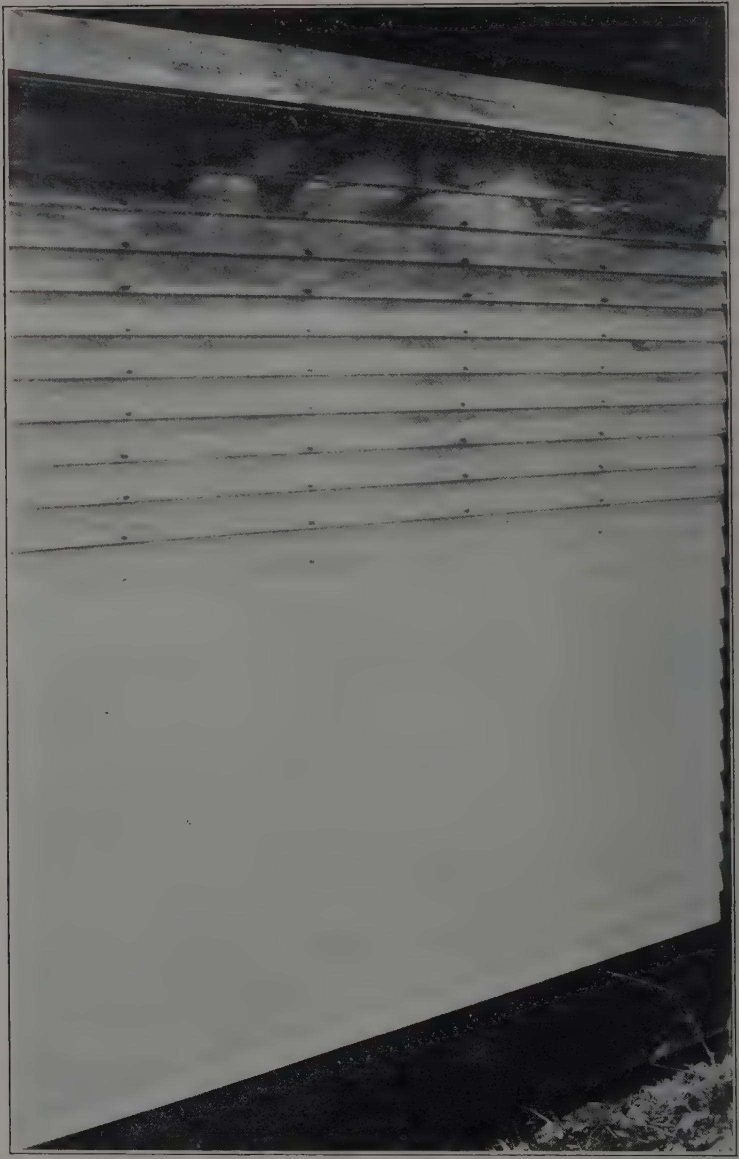

Fig. 22. Test Panel of Aspen Siding, Painted and Unpainted, After Ten Months' Exposure to Weather

ment. The properties of aspen and the results of tests now in progress indicate that it will meet requirements satisfactorily for exterior trim. Figure 22 shows painted and unpainted aspen siding after ten months' exposure to weather. Additional tests now started will furnish more detailed data on aspen exposed to the weather at widely scattered points throughout the United States.

Much exterior trim is narrow, that is, six inches or less in width. Aspen must go largely into uses that can utilize narrow stock, for the small size of the aspen tree results in the production of large amounts of narrow stock. Until a demand from specialized and exacting uses has developed, a portion of the cut will probably find a market locally as exterior trim.

Boxes and Crates

About 3½ billion board feet of softwoods and more than one billion feet of hardwoods were used in the United States in 1928 for boxes and crates.[13] This amounts to approximately 15 per cent of the total lumber cut annually. During recent years, the fiber carton and the veneer box have been used in increasing amounts. There seems to be little reason to believe, however, that the amount of lumber used for boxes will decrease very rapidly in the near future. As a matter of fact there are some indications that, as the number of people concentrated in urban and industrial centers increases and food and other goods must be shipped greater distances, the demands for boxes, crates, and other types of containers will increase.

To be used extensively for boxes and crates, a wood must have certain characteristics and properties, chief of which are: (1) lightness in weight, (2) strength, (3) nail-holding capacity, (4) appearance and workability, and (5) the absence of odor and taste. There is probably no such thing as an ideal wood for boxes and crates, but aspen seems to combine to a remarkable extent many of the required characteristics.

TABLE X

Average Specific Gravity of Various Woods and the Weight of Empty Boxes Corrected to 15 Per Cent Moisture Content

Species	Average specific gravity	Weight of empty box in pounds at 15 per cent moisture content
Aspen	0.362	6.33
Lowland white fir	.362	6 43
California red fir	.355	6.47
White fir	.363	6 54
Silver fir	.385	6.72
Western yellow pine	.393	7.16
Lodgepole pine	.437	7.63
Western hemlock	.432	8.16
Western larch	.562	9.44

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[13] The figures on the consumption of lumber for boxes and crates were obtained from a canvass conducted by the Forest Service in co-operation with the Bureau of the Census, United States Department of Commerce.

Aspen is one of the lightest of the hardwoods generally available for box shooks and crating material. A study made by the Forest Products Laboratory of the suitability of certain little-used woods for shipping containers shows that aspen produced the most serviceable box on the basis of weight of any of the species tested. The relative weight of the woods included in this study is given in Table X.

Altho aspen is not a strong wood, generally speaking, it possesses sufficient strength for all ordinary crating and boxing purposes. The bending strength of clear aspen is about the same as that of northern white pine and more than that of many other woods commonly used for boxes. Tests made from different woods show that boxes made of aspen are almost as satisfactory as those made of lodgepole and western yellow pine.

One of the most important considerations in using wooden containers for food products, such as cheese, butter, and fresh and smoked

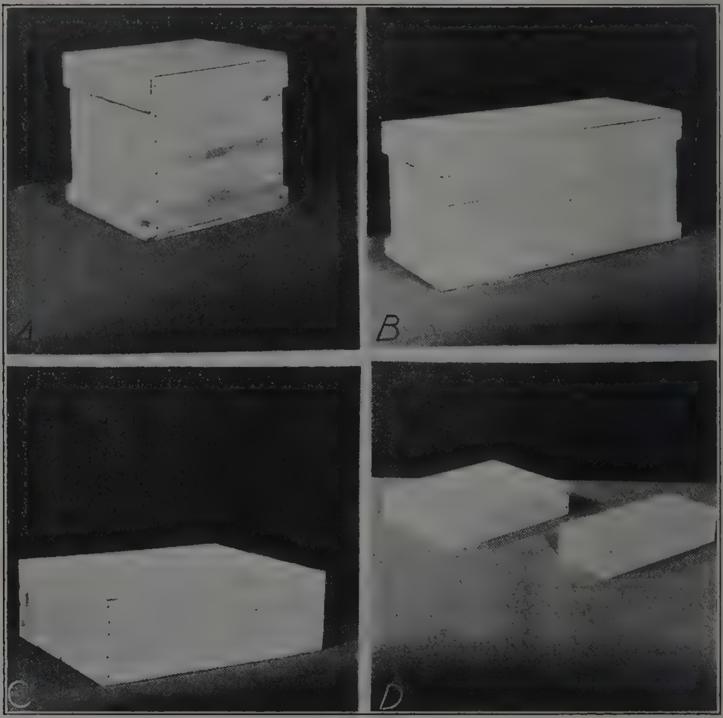

Fig. 23. Food Containers Made from Aspen
A. Farmers' heavy-duty egg case; fifteen-dozen size, made entirely of aspen.
B. Farmers' heavy-duty egg case, thirty-dozen size, made entirely from aspen.
C. Shipping box for dressed poultry made from aspen.
D. Cheese boxes, two- and four-pound sizes, made from aspen.

meats, is the absence of any pronounced odor and taste. Aspen wood is practically odorless and tasteless, and can be used with safety. The light color, soft texture, and smooth finish of the wood also adds much to the general appearance, so important in food containers.

Various types of boxes and crates made of aspen are shown in Figures 23 and 24. These have given very satisfactory service and there seems to be no reason why new and extended uses for these products can not be developed.

Minnesota, Michigan, and Wisconsin used about 554,000,000 board feet of lumber for boxes and crates in 1928. How much aspen contributed to this total is not known. In St. Paul and Minneapolis over 4,000,000 board feet of aspen were used for boxes and crates in 1928.

Excelsior

At the present time somewhat more than 200,000 cords of wood are used annually for the manufacture of excelsior. In the Lake States and New England States, where the industry is more concentrated, cottonwood and aspen are used extensively. Basswood, tho preferred, is used in smaller quantities. In the South and along the Atlantic seaboard, loblolly and shortleaf pines are used. Other woods used include western yellow pine and Douglas fir, particularly on the Pacific Coast; red gum in the South; and spruce, hemlock, and chestnut.

The qualities most desired in excelsior wood are toughness, light color, light weight, and freedom from odor. Basswood is generally believed to meet these requirements most fully, but scarcity and high prices militate against its wide use. It is estimated that not more than 11 per cent of the total annual production of excelsior is manufactured from basswood. Aspen wood meets all the essential requirements for excelsior; it is tough, white in color, comparatively straight grained, and free from odor. It is quite likely, therefore, that the use of aspen will continue to increase for the manufacture of excelsior.

A recent survey of wood requirements of the excelsior manufacturers of Wisconsin indicates that approximately 33,000 cords of aspen are used annually in that state. Minnesota manufactures only a comparatively small amount, but most of that which is manufactured is made from aspen. Figures on the use of aspen for excelsior manufacture in Michigan are not available, but as Michigan is one of the most important producers and aspen supplies are quite abundant, it is likely that a considerable quantity of aspen is used annually for excelsior.

The large production of excelsior in the state of Michigan is, no doubt, somewhat influenced by the requirements of the furniture industry of that state. Until additional local markets are found to

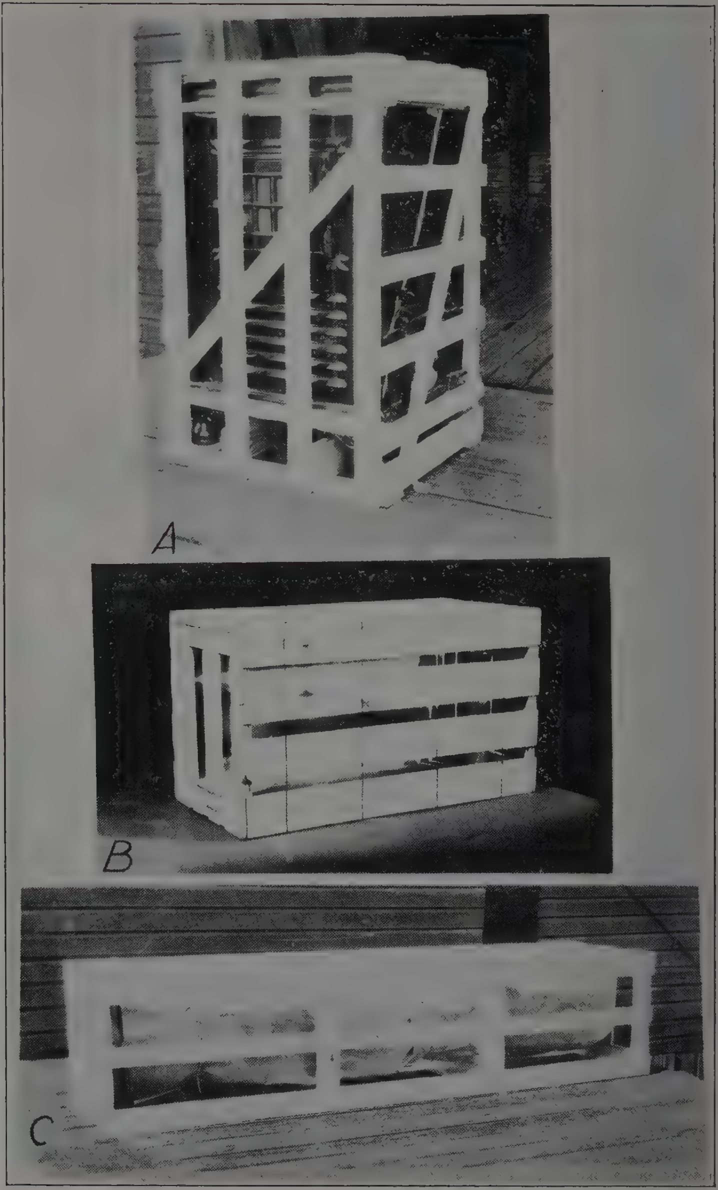

Fig. 24. Crates Made from Aspen
A. Aspen crate for home heater.
B. Wire-bound aspen crate.
C. Special design aspen crate for gasoline pump.

absorb the product, it is not likely that the output of excelsior in Minnesota will show very great increase. Large supplies of raw material, however, are available.

Crossties

At the present time more than 100,000,000 crossties are used annually in the United States. Altho the crosstie requirements of the country increased rapidly in the early years of railway building they are now declining, and will probably continue to decline to an annual requirement of from 65,000.000 to 75,000,000 crossties. This reduction is almost entirely owing to the use of wood preservatives, better track construction, and more adequate crosstie plating.

Nevertheless, crossties offer a large potential market for a wood that meets the requirements. The records available concerning the service of aspen crossties are encouraging.

To give satisfactory service as a crosstie, a wood must be (1) decay resistant, or made so through preservative treatment, (2) able to resist impact, (3) able to resist spike pulling, and (4) it must be of sufficient strength to withstand the strains of center binding.

There are no simple mechanical tests that can be made of wood to determine its exact value for crossties. Some composite tests to approximate this value, however, have been made by the Forest Products Laboratory. These tests involve (1) static and impact bending, (2) compression parallel to the grain and end hardness, and (3) compression perpendicular to the grain and side hardness. On the basis of these tests, some common crosstie woods were classified. These results are given in Table XI. In the use and interpretation of the data, it must be borne in mind that the figures are approximations and that the mechanical properties of individual pieces of any species may

TABLE XI

Mechanical Properties of Various Species of Wood Used for Crossties

Species	Composite figure
White oak (commercial)	103
Longleaf pine	95
Western larch	80
Douglas fir (coast type)	78
Tamarack	71
Douglas fir (Rocky Mountain type)	65
Jack pine	58
Lodgepole pine	56
Poplar, yellow	55
Largetooth aspen	53
Western red cedar	52
Cottonwood, eastern	49
Aspen	46
Northern white cedar	40

vary as much as 30 per cent either above or below this average value. In Table XI a high composite value is indication of desirable mechanical properties for crosstie purposes.

The composite values indicate that aspen crossties posses mechanical properties somewhat similar to those of northern white cedar, and common cottonwood. Because northern white cedar crossties have given satisfactory service on tangents and switches on lines carrying light traffic, it is reasonable to suppose that aspen ties, properly plated and treated, would give similarly satisfactory service under the same conditions.

Except under very unusual conditions, aspen crossties must be treated with a preservative to give satisfactory service. No data are available giving the life of untreated aspen crossties, but there is reason to believe that under conditions conducive to decay their average life will not be in excess of two or three years. As aspen ties have not been used extensively, few records of service are available.

In 1914, a large Canadian railway system installed a small number of aspen crossties in its tracks near Pembroke, Ontario, where the traffic is not heavy. These crossties were treated with a mixture of creosote-coal tar solution containing 70 per cent creosote and 30 per cent coal tar. The amount of absorption of preservative by these crossties is not stated. At the last inspection, these ties were still giving good service and did not show signs of excessive rail cutting.

In the fall of 1925, the same Canadian railway system let one contract for the delivery of 200,000 aspen crossties in Alberta. Only 45,000 crossties were delivered on this contract because of the prevalence of "black heart" in the aspen from Alberta. At the same time another contract was let for 50,000 crossties. These were delivered, but were also found to contain "black heart." The purchase of aspen crossties by the railway was therefore discontinued, owing entirely to the prevalence of "black heart."

The crossties obtained under these contracts were square sawed, 7 by 9 inches by 8 feet, 7 by 8 inches by 8 feet, and a few were 6 by 7 inches by 8 feet. All crossties were adzed, bored, and incised, and were treated by the "Rueping Process" with a net retention of six pounds of 70-30 creosote-coal tar solution per cubic foot. No difficulty was experienced in making the treatments. The average penetration was about one inch and the distribution of oil in the crossties was uniform. Information is lacking on the treatment of aspen crossties with water soluble preservatives, such as zinc chloride. It is known, however, that aspen fence posts may be rather easily treated with this salt, and there is no apparent reason why aspen crossties should resist treatment with zinc chloride solution.

Altho experience with the use of aspen crossties is limited, it appears that when properly treated they will give satisfactory service when placed in lines over which traffic is not too heavy. It further appears that the greatest obstacle in using aspen for crossties is the prevalence of "black heart," or common heart rot.

If aspen crossties are cut extensively in the Lake States, care must be taken to prevent fungous infection between the time of cutting and treating. Even aspen heartwood is very susceptible to decay. For this reason, it is recommended that aspen crossties be cut during the winter months and seasoned carefully. Preservative treatment should be given as soon as possible after the ties are in proper condition for treatment.

Fuel Wood

It is estimated that 100,000,000 cords of fuel wood are used annually in the United States. Of this amount about 36,000,000 cords are produced on farms. In 1925, about 1,154,000 cords of wood were cut on Minnesota farms; about 1,858,000 cords on Wisconsin farms; and about 1,368,000 cords of fuel wood on Michigan farms.

In all probability only a comparatively small amount of aspen is cut in any of the Lake States for fuel. This, in part at least, is no doubt influenced by the fact that by far the larger stands of aspen are found in the sparsely settled regions of the Lake States. In many respects, aspen makes a good fuel wood. When green, the tree cuts and splits easily, dries out rapidly, and burns with a steady flame. On a weight basis, it gives about as much heat as any other non-resinous wood; that is, a ton of dry aspen yields about as much heat in burning as a ton of hickory or oak. In Table XII are given the fuel values of some common woods. The values are for dry, or comparatively dry woods. The heating value of wood containing larger amounts of moisture is materially reduced and the vigor with which the wood burns is much less. Fire wood should, therefore, be well seasoned before it is used.

On the average, a pound of dry wood liberates on combustion approximately 8,000 B.t.u., bituminous coal 13,000, anthracite coal about 13,000, and charcoal about 16,000 B.t.u. Fuel wood is ordinarily not sold by weight but by volume. A cord of aspen wood will give up on burning cnly about half the total amount of heat of a cord of white oak or hickory. A cord of dry hickory wood is about equivalent in heating value to a ton of coal, whereas a cord of aspen is about equivalent to one-half ton of coal in heating value.

Even dry wood is, however, a much less concentrated fuel than coal or oil. For this reason, combined with handling costs, it can not be transported long distances and the use of wood as a domestic fuel in urban centers is usually a luxury.

TABLE XII

HEAT VALUES OF CORDWOOD—WEIGHTS FOR OVEN-DRY, AIR-DRY, AND GREEN WOODS, AND ASSUMING 7,350 B.T.U. AVAILABLE PER POUND OF DRY WOOD WITH FLUE GASES AT 300° F.

Species	Available heat units per cord of 90 solid cubic feet (in millions B.t.u.)	
	Air-dry	Green
Hardwoods		
Ash, white (*F. americana*)	20.5	19.9
Aspen, (*F. tremuloides*)	14.1	12.1
Aspen, largetooth (*P. grandidentata*)	14.2	12.4
Basswood, (*T. americana*)	12.6	11.0
Beech, (*F. atropnicea*)	20.9	19.7
Birch, paper (*B. papyrifera*)	18.2	16.7
Birch, yellow (*B. lutea*)	20.9	19.4
Cottonwood, eastern (*P. deltoides*)	15.0	12.7
Maple, sugar (*A. saccharum*)	21.8	20.4
Oak, red (*Q. rubra*)	21.7	19.6
Oak, white (*Q. alba*)	23.9	22.4
Softwoods		
Hemlock, eastern (*T. canadensis*)	15.0	12.8
Pine, jack (*P. divaricata*)	15.7	13.4
Pine, Norway (*P. resinosa*)	17.8	16.8
Coal, long ton (2,240 pounds)	29.1	

* Based on Forest Products Laboratory tests.

Posts

Practically all woods are used for fence posts. A decided preference exists, however, for naturally decay-resistant woods. When these are not available at reasonable prices, posts made of woods lacking natural decay resistance may be used but they should be treated with a preservative. The number of posts required annually in the Lake States is not known, but it probably exceeds 100,000,000. In the United States as a whole, it is estimated that approximately 900,000,000 posts are needed annually.

In Minnesota, aspen fence posts are often used either in their natural condition or treated with a preservative. The average life of an untreated aspen post in the Lake States region is estimated to be from three to six years, depending upon the locality, soil condition, and size of the post. In a semi-arid region aspen posts last much longer.

The average life of creosoted aspen posts is not known. Pressure-treated aspen posts, in tests at the Forest Products Laboratory in co-operation with the University of Wisconsin, were in good condition after thirteen years of service, and will undoubtedly give many more years of service. An estimated average life of 20 to 25 years for properly pressure-creosoted aspen fence posts is thought to be conservative. The posts included in the Wisconsin test absorbed in excess 16 pounds of creosote per cubic foot or approximately two gallons per post. The absorption can be regulated by proper control of the treating conditions. The hot and cold bath process may be used with aspen posts, altho the absorption of the preservative and depth of penetration are not subject to so close control as in pressure treating.

The use of aspen for posts in the Lake States will undoubetdly increase as the more desirable species become scarcer and consequently more expensive. This use probably will have little influence on the general problem, as there are few localities where the production of fence posts forms an industry. More often fence posts are cut by the farmer as the need occurs. Aspen is a common tree in farm woodlots in many sections of the Lake States, and these woodlots will undoubtedly provide a large part of the future demand for fence posts.

Mine Timbers

In 1923, 13,000,000 cubic feet of round, and 20,000,000 board feet of sawed mine timbers were used in the Lake States, principally in Michigan and Minnesota. Altho a comparatively small portion of aspen is used for mine timbers in the Lake States, it is suitable for that purpose. The two outstanding qualifications required of mine timbers are adequate strength and reasonable resistance to decay. Lack of natural decay resistance, however, can be overcome with preservative treatment.

Ordinarily round mine timbers are not graded for either strength or appearance, but in the mining industry there has developed a very definite conception of what species are suitable or at least desirable for the mine timbers. This method of evaluation of the suitability of a species for mine timbers undoubtedly militates against a wider use of aspen for this purpose.

A study of the suitability of different woods for mine timbers has been made by the Forest Products Laboratory, Forest Service, Madison, Wisconsin. The various woods used for mine timbers were classified into five groups based upon a combination of strength properties. These properties are strength as a beam or a post, and toughness or shock resistance. The species were first grouped as to strength as a beam or a post; toughness was then considered and all species ranking low in this property were placed in one group because timbers low in toughness do not give warning of failure.

The average strength of each group is seven eighths of the average of the next higher group. Within each group the species are arranged alphabetically.

The hardwoods listed in Groups I and II are seldom used for mine timbers if other markets are available. This results in the inferior or smaller pieces reaching the mines. Mine timbers of several woods

Group I

Ash, white
Beech
Birch, sweet
Birch, yellow
Douglas fir (dense coast type)
Elm, rock
Larch, western
Maple, red
Maple, sugar
Oak, commercial white
Oak, commercial red
Pine, (dense southern yellow)

Group II

Ash, pumpkin
Cedar, Port Oxford
Cypress, southern
Douglas fir (Rocky Mountain type)
Douglas fir (sound coast type)
Elm, slippery
Elm, American
Gum, black
Gum, tupelo
Gum, red
Hackberry
Hemlock, eastern
Hemlock, western
Magnolia, cucumber
Magnolia (evergreen)
Pine, Norway
Pine, (sound southern yellow)
Tamarack

Group III

Ash, black
Birch, paper
Fir, silver
Fir, noble
Maple, silver
Pine, lodgepole
Pine, northern white
Pine, western white
Spruce, red
Spruce, white
Spruce, Sitka
Sycamore

Group IV

Basswood
Butternut
Cedar, incense
Cedar, western red
Chestnut
Cottonwood, eastern
Fir, white
Pine, jack
Pine, limber
Pine, sugar
Pine, western yellow
Pinon
Poplar, yellow

Group V

Aspen
Buckeye, yellow
Cedar, northern white
Cedar, southern white
Fir, Alpine
Fir, balsam
Spruce, Engelmann
Willow, black

listed in Groups III, IV, and V represent mill or woods run, and consequently show a wide range in strength. The best and strongest material, except for a few species, will not have been sorted for other uses. Sawed mine timbers from Groups III, IV, and V will, therefore, often average better in grade, other things being equal, than those from the Groups I and II. In selecting aspen mine timbers, care must be taken not to include pieces having advanced stages or extensive heart rot. In the storage of aspen mine timbers, precaution must be taken to prevent decay. Removing the bark immediately after cutting and piling to facilitate rapid seasoning will help. As aspen mine timbers are susceptible to decay, unless used temporarily, they should be treated with preservatives.

Slack Cooperage

Aspen has been used to some extent in Minnesota for slack cooperage, particularly for barrels, for the shipment of flour. At the present time there seems to be little or no demand in the Lake States for this type of container and little evidence that it will increase. The cloth sack and the paper bag have almost entirely replaced barrels for the shipment of flour.

Slack cooperage is also used for sugar, fruits, cranberries, candy, chemicals, and other commodities. Quantities of some of these commodities are produced in the Lake States, which suggests that a market may exist for a small amount of slack cooperage. Whether aspen will be used for containers for all of these commodities is doubtful. It is also doubtful if aspen can compete in price with such woods as red gum, elm, and pine. The small size of the aspen trees and the numerous defects prevent its extended use for cooperage purposes. It appears, however, that aspen may compete successfully with other woods for slack cooperage heading. Basswood is generally preferred for this purpose because of its toughness, light color, light weight, and freedom from odor. As heading stock need not be so large as stave stock, no difficulty should be experienced in securing stock for aspen heading that is free from serious defects.

Tight Cooperage

Tight cooperage is extensively used for the shipment of liquids and food substance of various kinds. It is not likely that aspen will be used extensively for this purpose in the Lake States because of its many defects and small size. Aspen may prove satisfactory, however, for the manufacture of certain smaller types of tight cooperage.

Matches

The use of aspen wood in the manufacture of matches in this country is just beginning. The match industry offers a new and large field for the use of aspen after production is on a permanent and large enough scale.

Core Stock

A large amount of furniture is manufactured in the Lake States. Furniture manufacturers are looking more and more for new woods for core stock as the woods they are now using become scarcer and higher in price. The possibility of using aspen for core stock may, therefore, well be considered. Aspen can be delivered to Lake States furniture manufacturers with a comparatively short haul and accompanying low transportation costs.

One of the properties required of wood for core stock is a capacity to take and hold glue. None of the woods extensively used at present and none that have been tested so far excel aspen in this respect. Light weight, ability to stay in place, ease of working, and small shrinkage are additional desirable properties of aspen for core stock. Uniform texture and absence of a tendency of the grain to rise give it an advantage over most soft woods used for this purpose.

Novelties

Because of its physical and mechanical properties, aspen should find favor with industries manufacturing various novelties. Clothespins are manufactured successfully from aspen wood (Fig. 25). There is no reason why aspen could not be used for spools, tongue depressers, swab sticks, skewers, toy stock, and a many other articles. Economic conditions and markets, rather than the technical properties of wood, will probably largely determine the development of these uses of aspen.

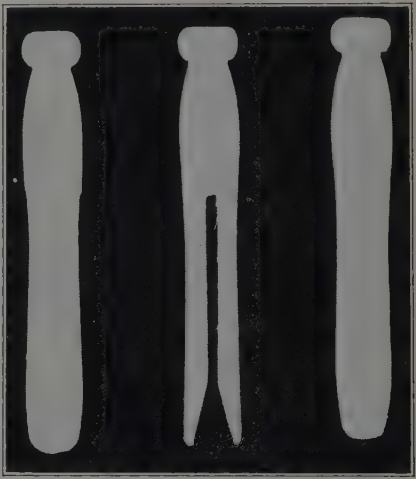

Fig. 25. Aspen Clothespins

Aspen in Pulp and Paper Industry

In 1926 it was estimated that approximately 33,000 cords of aspen pulp wood were used in the entire Lake States. Three years later it was estimated that over 100,000 cords of aspen pulp wood were used in Minnesota alone. Altho this increase may not be general throughout the Lake States, it does indicate that the demand for aspen pulp is increasing.

In Minnesota, the 1930 aspen stumpage prices range from 25 cents to $1 per cord, depending upon the quantity, quality, and accessibility. At the mills, aspen pulp wood brings from $8.50 to $9 per cord of peeled wood. Prices at shipping points are usually equivalent to mill prices less the freight to the mill.

In the Lake States at present, aspen is used extensively for the manufacture of soda pulp. Because of the fact that mills already established in the East are able to supply the existing demand for soda pulp, it is not likely that the production of soda pulp in the Lake States will increase greatly in the immediate future.

Aspen now is used in the sulphite process to produce pulps having specific properties, such as bulk, opacity, and softness. This pulp is used in the manufacture of books, tissue, and specialty papers. There are indications that the output of this type of paper will materially increase. It has been proved by the Forest Products Laboratory that aspen sulphite can be substituted to some extent for spruce and hemlock sulphite, and that it is possible to digest aspen and coniferous woods in the same digester. A small amount of aspen is now ground for newsprint and for pulp boards, and it is possible that this use may increase. Aspen is also used to a small extent in semichemical and semimechanical processes.

On the whole it appears that the future utilization of aspen for pulping depends on its use in the standard pulping methods. These methods will undoubtedly be slightly modified from time to time to produce the kinds of pulp that are most in demand in the paper market. It is believed that large quantities of aspen will eventually be used by the paper industry, thereby giving an important outlet for the vast aspen resources of the region.

Other Uses of Aspen

In addition to the uses previously referred to, aspen has also been used to a small extent for a great variety of products. No detailed information seems to be available concerning the suitability of aspen in the manufacture of these products other than that it has been used. Some of these uses for aspen are:

Baskets, fruit and vegetable packages
Beams and frames for railroad cars
Blocks, brush
Boards, hosiery
Boats, stone
Bodies, vehicle
Bottoms, basket
Boxes and crates
Boxes, bluing
Boxes, butter
Boxes, candy
Boxes, cheese
Box, lock-cornered

Boxes, piano
Boxes, pill
Boxes, shoe peg
Boxes, tackle
Boxes, veneer
Brooms
Brushes
Buckets
Cabinets
Carriers, potato
Carriers, root
Cases, shipping
Casing
Casing, house
Caskets and outside boxes
Ceiling
Clapboards
Cooperage
Crates
Crating
Doors
Dowels and skewers
Dressers
Driers, clothes
Excelsior
Fillers, shoe
Finish, interior, house
Fixtures
Flooring
Forms, hosiery
Forms, shoe
Frames, door
Frames, window
Furniture
Furniture, work, hidden
Games
Handles, brush
Handles, cutlery
Handles, dipper
Handles, knife, oyster
Handles, paint and sweeping
Heads, spool
Hoops, basket
Implements, agricultural
Kegs, putty
Kegs, spice
Kits, fish
Ladders
Lasts, shoe
Lining, interior, refrigerator
Matches
Novelties
Newels, stair
Organs
Pails, candy
Pails, cooky
Parts, body, vehicle, machinery
Parts, organ
Parts, potato machinery
Poles
Products, planing mill
Pulp, paper
Racks, clothes
Refrigerators
Sash, doors, and blinds
Scows, sand
Sheathing
Sheeting
Shingles
Shooks
Shuttles, spools and bobbins
Siding
Sleds, bob
Spools
Stringers
Stringers, clothes rack
Supplies, dispensary
Sweepers, carpet
Tenders, baby
Timbers, mine
Toothpicks
Toys, bottom, cart
Toys, bottom, sled
Toys, bottom, wagon
Toys, game
Toys, wheelbarrow
Toys, yard, play, baby
Trees, show
Tubs, food, poultry
Tubs, jelly
Tubs, lard
Tubs, powder
Tubs, sugar
Vehicle parts
Woodenware
Wool, wood
Work, interior, furniture

Extending the Market for Aspen

Altho aspen may still be regarded as a little-used species, considerable progress has been made in extending its field of usefulness. Aspen has certain characteristics that make it suitable for many uses. The real problem of extending the market for aspen appears to consist largely in acquainting the wood-using industries with the characteristics of the wood and in the recognition of the possibilities for its use.

Industry, however, accepts new woods slowly, and prejudice and custom are difficult to overcome. The most effective way is to accumulate, through research, all the facts dealing with the physical and mechanical properties of the wood. A considerable amount of this work has already been done, but much still remains. The accumulation of facts is not enough. Aspen wood must actually be used for specific purposes, and its suitability for these purposes determined. This type of work has been, and probably will continue to be, done largely by progressive lumber manufacturers.

Wood-using industries should co-operate in these efforts, at least to the extent of maintaining an open mind to the possibilities. Wood-using industries, manufacturing products for which aspen might be suitable might advantageously secure a small shipment of wood and use it in an experimental way. No other single procedure would contribute more towards the rational utilization of wood. New markets for little-used woods are generally mutually advantageous to both the lumber producer and the lumber consumer.

Research agencies and educational institutions can also participate and co-operate in trade extension activities by analyzing the problems confronting the wood-using industries and interpreting their needs in the light of the known facts concerning the properties of various woods. These agencies should at all times be alert to the opportunities to render service to the lumber and wood-using industries and should be so organized and supported that they will be able to respond to the demands made on them.

CONCLUSIONS

The large area of land occupied by aspen forests in the Lake States makes it essential that the species be utilized more extensively. The wood is growing faster than it is being used, and the short life of the tree requires that consumption be more nearly balanced with growth; otherwise large portions of the crop will be wasted.

Aspen is a forest crop from which a profit can be obtained if good judgment is used and the available information is applied to the existing aspen stands.

The clear wood of aspen has many excellent properties. The properties adapt it better to uses where light weight, softness, ease of working, and good gluing and good painting characteristics are desired rather than to uses where great strength and decay resistance are required. The species is better adapted to specialty than to general use requirements.

Regardless of the many excellent properties of the clear wood, uses other than lumber must be relied on for the utilization of the bulk of aspen stands in the Lake States. The small size of the tree and its susceptibility to decay make it difficult to log and mill at a profit. Even under the best of practice the proportion of the higher and profitable grades will be low. The present small production of aspen lumber is therefore due to the size of the tree and yield in grades, and not to inferior properties of the wood.

Dimension stock, that is, stock cut to size at the mill, apparently offers better prospects for marketing aspen at a profit than does yard lumber. The tendency toward the production of dimension stock is increasing. Dimension stock is particularly adapted to the production of small clear pieces in which form aspen is most attractive and it offers a possibility of converting the unprofitable low grades into a more profitable form.

There are good possibilities of marketing aspen at a profit in forms other than lumber. The small size of the tree does not handicap the marketing of the species for pulp wood, excelsior, fence posts, and mine props as it does for lumber. The cost of delivering wood as raw material is much lower than that involved in delivering lumber to users, and the chances of marketing aspen at a profit are therefore better. Recent experiments with new methods of pulping tend to increase its possibilities as a pulp wood. Aspen mixed with eastern hemlock or eastern spruce for the manufacture of sulphite pulp is the most promising possibility for increased utilization of the aspen of the Lake States. Preservative treatment of mine timber and fence posts offer opportunities of increasing the consumption of aspen for these purposes. The Lake States, producing the largest amount of excelsior, offer an excellent market for aspen, especially as it is one of the preferred woods for this purpose. There is, however, small prospect of a material increase in this use.

It is to be expected, therefore, that the bulk of the aspen crop will be marketed as a primary product rather than as lumber.

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University of Minnesota
Agricultural Experiment Station

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William B. Owen
Division of Entomology and Economic Zoology

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FACTORS THAT INFLUENCE THE DEVELOPMENT AND SURVIVAL OF THE OVA OF AN ASCARID ROUNDWORM TOXOCARA CANIS (WERNER, 1782) STILES, 1905[1] UNDER FIELD CONDITIONS

William B. Owen

INTRODUCTION

Parasitic infections of domesticated animals are a problem of much economic importance, but information concerning infections arising from parasites lodged in the soil is meager and generally derived in a large part from the study of the parasites of man. With the growing importance of the fur-farming industry in this country there has arisen a demand for more exact information regarding the species affecting foxes and other animals that are reared under pen conditions.

Among the most common of the parasitic worms affecting foxes and other carnivors are the ascarid roundworms. Those found in foxes are very closely related to, and in most cases identical with, *Toxocara canis* of the dog. They have long been recognized as a source of loss to breeders, and as particularly dangerous to young animals. The more modern work has shown that the early larval stages undergo a complicated migration through the tissues of the animal and that in this period they may cause the death of their host in a hitherto unsuspected way.

As is well known, new infections under natural conditions result from the animal swallowing ova which have been incubated in the soil or water. A practical question often asked by fur farmers is regarding the length of time that the ova of the worms may be expected to remain viable in the soil of animal pens. It is obviously important to determine what factor or factors govern development and survival under these conditions.

To give a satisfactory answer to this question, based upon careful observations, the author carried on the studies here described. The studies on survival of ova during the winter months in the region of

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[1] The writer wishes to express his sincerest appreciation to Dr. William A. Riley, Division of Entomology and Economic Zoology, for his helpful suggestions and encouragement during the course of the studies herein described. Acknowledgment is also made to Dr. Royal N. Chapman and to Mr. Allan Mail, of the Division of Entomology and Economic Zoology for placing at the writer's disposal various equipment and the thermocouple data on soil temperature.

Minneapolis, Minnesota, were supplemented with some tests on survival at low temperature under laboratory conditions. The studies on survival under summer conditions were extended to include a single experiment carried out in western Kentucky. Some data on development in air of known moisture content are also given.

ECONOMIC ASPECTS OF THE PROBLEM

The longevity of the ova of the ascarid worms in the soil is not only of biological interest but has a definite practical bearing on the problems of incidence of parasitism and renewed infection after anthelminthic treatment. Animal breeders frequently find that shortly after anthelminthic treatment their animals again become heavily parasitized. In fact, if soil where animals run, floors of pens, and bedding are contaminated with the infective ova of the worms, administration of anthelminthics can give only temporary relief. Thus far in prophylactic studies, a satisfactory method for sterilizing soil on a large scale in pens and pastures has not been found. The opinion is frequently held by many breeders of foxes that the low temperatures during the winter months in our northern states is severe enough to kill the ova that are exposed on the floors of animal pens. One phase of the present problem has been to test the validity of this much advocated idea, for, if it is true, an obvious and practical method of making pens safe would be to remove animals in the fall so as to prevent daily accession of ova and allow those present to be killed by the unfavorable weather conditions. If it is possible to establish a criterion for the survival of the ova of the ascarid worms under field conditions during the different seasons of the year, then a step will have been made toward the solution of the problem of soil infections in these forms.

HISTORICAL ACCOUNT

In the works of early helminthologists, frequent reference is made to the longevity of ascarid ova. Verloren (1854) kept the ova of *Ascaris marginata* (*Toxocara canis*) in water for more than a year and yet they were alive. Richter, as reported by Küchenmeister (1857), placed the ova of this species in water and found that they contained living embryos eleven months later. Davaine (1863) reports that the ova of *Ascaris lumbricoides* were alive after being stored for a period of five years. None of these writers give exact details as to the conditions under which the tests were made. These experiments are not strictly comparable with the studies reported here, yet they do emphasize the fact that ascarid ova may remain alive under certain conditions for one year or more.

Studies on related species, which have a more direct bearing on the present problem, are to be found only in recent literature. Yoshida (1920) placed the ova of *Ascaris lumbricoides* on the surface of the soil and under a thin layer of soil and allowed them to remain during the winter months at Osaka, Japan. Experimental feeding of these ova to a guinea pig at the end of this period proved that they were alive. Martin (1922) reports that the ova of *Ascaris suum* survived in the soil during the winter months in Nebraska. McCulloch, Graham, and Carroll (1927) failed to find viable *Ascaris suum* ova after eight months' exposure in the soil at Urbana, Illinois. On the other hand, Raffensperger (1927) reports that in one experiment the ova of this same species survived for one year under field conditions at Chicago, Illinois. None of the above mentioned writers have given actual soil temperature records for the period of exposure.

More critical studies on this problem, which take into consideration the different environmental factors that may influence development and survival of ascarid ova, are as follows: Brown (1927) found that the development and survival of the ova of *Ascaris lumbricoides* under field conditions in Panama were governed by the type of soil in which exposed and whether they received full sunlight or were in the shade for the period of exposure. Caldwell and Caldwell (1928) report experiments carried on in Alabama during the month of July, in which the ova of *Ascaris lumbricoides,* in fecal plants on different types of soil, disintegrated on three days of exposure to full sunlight. Ova in like cultures, but placed under shade conditions, were relatively unaffected when examined more than a month later. Viable ova were recovered from soil cultures which had been under natural conditions from August until the following May. Brown (1928) reports that the ova of *Ascaris lumbricoides* and *Ascaris suum* survived in sand cultures under weather conditions at Baltimore, Maryland, from December 30 to May 2. Riley and Owen (1928) and also Owen (1928, preliminary report) found that the ova of *Toxocara canis* survived in the soil under field conditions in the region of Minneapolis, Minnesota, from November 11 to April 26.

MATERIALS AND METHODS

Toxocara canis was selected as the object of these studies because of its high incidence and close relationship to some of the other roundworms found in a number of domesticated carnivors. It is a common parasite of dogs, which afford a convenient source for the collection of the adult worms.

In planning each experiment, attempts were made to expose the ova in outdoor cultures which would be comparable with conditions they would normally encounter in nature. The ova were collected from the uteri of gravid females. Only those ova from the terminal portion of the uteri that were known to be fully mature were used. The culture plots in which they were planted were prepared from different types of soil—sand, clay, and humus. Small flower pots, 3:5 inches in diameter at the top and 4 inches in depth, were filled with the desired type of soil and sunk into the ground to such a depth that the surface of the soil in the container was on the same level as that of the surrounding ground. The ova were placed on the surface of the soil in the container or mixed with the upper half inch of soil stratum, depending on the condition desired. No exact estimate of the number of ova planted in each culture was made; however, an approximate estimate would be about 75,000. In every experiment performed, a number of the ova were cultured at 25 degrees centigrade as a check to determine whether they were fertile.

The records of soil temperature during the winter months were obtained with a standard copper-constantan thermocouple. The winter cultures were placed about eight inches from the instrument. The soil temperature records for the summer cultures were obtained with a mercury thermometer.

To facilitate the making of differential counts after ova were recovered from the soil, the isolation method used by Caldwell and Caldwell (1928) and in part, that described by Spindler (1929), was used. This method briefly consists of (1) treating a soil sample containing ova with a 30 per cent antiformin solution to free them from soil particles, and (2) floating the ova from the material with a solution of high specific gravity, as concentrated sugar solution or sodium dichromate. In these studies sodium dichromate was used to float the ova from a treated soil sample. The surface film of this mixture is looped off with the open end of a small test tube, transferred to a glass slide, and examined with a 16 mm. objective. In the tables of results, the ova are classified upon the basis of their developmental progress and state, i.e., disintegrated, morula, motile embryos. After certain experiments, infection tests were made on guinea pigs and laboratory rats to determine the viability of the motile embryo state.

SURVIVAL UNDER WINTER CONDITIONS IN MINNESOTA[2]

To obtain the data on survival of ova under winter conditions in Minnesota, three cultures, using sand, clay, and humus soil as media, were prepared on November 11, 1927, and placed for exposure on University Farm. The ova in an unsegmented state were mixed with the upper half-inch soil stratum in each culture, thus making the conditions comparable with those to which they would normally be subjected in nature. On April 26, 1928, the cultures were brought into the laboratory for observation. At this time, a number of the ova were isolated from a soil sample. None showed further development. Obviously, because of the low temperature they had remained dormant during the entire period of exposure. The cultures were then placed in an incubator, which was maintained at 25° C. until May 12, when the ova were isolated and final differential counts were made. The results of this experiment are given in Table I.

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[2] A brief report of this experiment was published by Riley and Owen (1928) and also by Owen (1928).

TABLE I

DEVELOPMENT SHOWN BY THE OVA OF *Toxocara canis* AFTER EXPOSURE TO FIELD CONDITIONS FROM NOVEMBER 11, 1927, TO APRIL 26, 1928

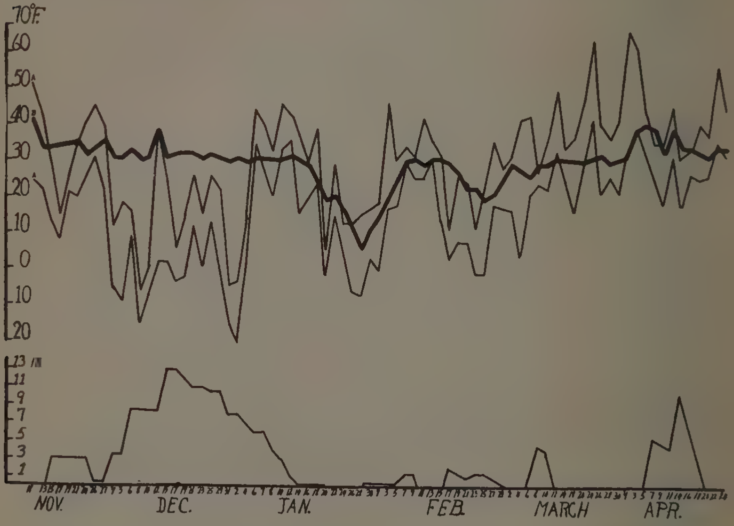
Culture	Number counted	Undeveloped	Morula*	Vermiform	Motile embryos	Dead
		per cent	per cent	per cent	per cent	per cent
Humus	200	13.0	4.5	6.0	74.0	2.5
Clay	200	4.5	0.5	11.0	79.0	5.0
Sand	200	4.5	5.0	8.5	80.0	2.0

* For convenience, the term morula is used in this report to designate all multicellular developmental phases previous to the vermiform stage.

Consideration of these data shows that from 74 to 80 per cent of the ova developed motile embryos with only sixteen days' incubation, after the cultures were placed at a temperature of 25° C. From 84 to 93 per cent were viable, as is shown by the proportion in developmental stages at the time the counts were made. These data coincide very closely in all the cultures. The differences are probably owing to the technic of recovering ova from the soil rather than to any influence the type of soil exerted.

To test whether these motile larvae were reduced in vitality by the ova having been subjected to the temperature indicated in Graph 1 and remaining dormant in the unsegmented condition for more than five months previous to development, about 500 were fed to a young laboratory rat. At the expiration of three days, the lungs and liver were examined with a Baermann isolating apparatus for migrating larvae. Four larvae were recovered. This number seems small, but when compared with the results of Scott (1928) on recovering hookworm larvae from the organs of the host by the same method, it is significant.

Graph 1 indicates the physical conditions of the environment during the course of the experiment. The soil temperature readings were taken on alternate days. The air temperature curves were plotted from readings taken on the days the soil temperature was recorded. Graph 1 illustrates some significant points to be taken into consideration in a study of field conditions during the winter months in any of the northern states. Snow and, to a less extent, ice serve as a blanket to keep the superficial soil temperature from fluctuating as does the air temperature. Records show that the weather conditions of December were the most severe in years, having 22.8 inches of unmelted snowfall and a mean air temperature of 7.34° F. (—13.7° C.). The lowest recorded air temperature for December was —15° F. (—26.11° C.). On the day this record was obtained the soil temperature under 5.5 inches of snow was 31.64° F. (—0.23° C.). The lowest recorded air temperature for the entire period was —20.0° F. (—28.89° C.). On this date the soil temperature under 5 inches of snow was again 31.64° F. (—0.23° C.). The lowest recorded soil temperature during the entire period was 6.26° F. (—14.33° C.). The air temperature on this date was —6.0° F. (—21.11° C.). These data clearly demonstrate that in a region of much snowfall, air temperatures are not a true index to the temperature conditions on the surface of the soil.



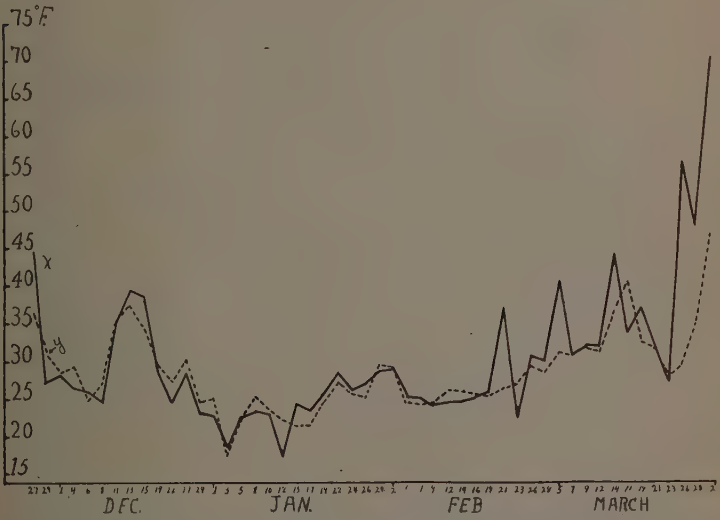
Graph 1. Air Temperature, Soil Temperature, and Snowfall from November 11, 1927 to April 24, 1928

Explanation: A, maximum air temperature; A′, minimum air temperature; and B, soil temperature at two inches beneath the surface. (No provision for surface soil temperature records was made during this season.) Snowfall is shown in inches. The air temperature data are from the United States Weather Bureau, Minneapolis station. The soil temperature data are thermocouple readings taken at site of the cultures. The snowfall was likewise measured at site of cultures.

During the winter of 1928 and 1929, soil temperature records were kept with the same apparatus, to which was added a surface junction. The records of this season are given in Graph 2.

Comparison of the figures from the surface with those from two inches beneath the surface indicate that there was little difference in the temperature at the two levels. It is interesting to note that the lowest temperature recorded on the surface of the soil during the winter of 1928-29 was 17.24° F. (—8.2° C.). Records of soil temperature during the winter months of two consecutive years show that at no time did it become cold enough to kill the ova of this species, as shall be seen from laboratory tests on viability at low temperatures.

Data from current studies on the resistance of helminth eggs to weather conditions do not as a rule take into consideration the striking contrast between air and soil temperatures during the season of heavy snows. It is obvious from the above data that air temperature readings alone, when considered apart from other physical factors, can not be relied upon during the winter months to give a true picture of conditions on the surface of the soil.



Graph 2. Soil Temperature Records from November 27, 1928 to April 2, 1929
Explanation: X, soil temperature at the surface; Y, soil temperature at two inches beneath the surface. Data taken from thermocouple readings.

DEVELOPMENT AND SURVIVAL UNDER SUMMER CONDITIONS

In Minnesota

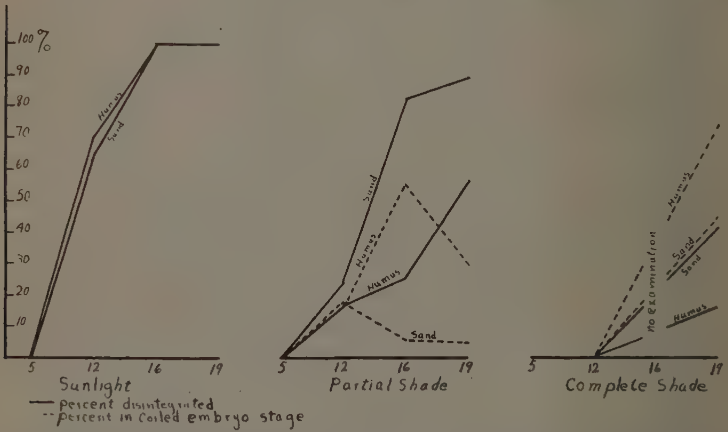
The studies on the development and survival of the ova of this species under summer conditions in Minnesota were begun during the season of 1928. On May 11 of that year, ova in an unsegmented condition were placed on the surface of cultures that were prepared from sand, clay, and humus soil, respectively. As these ova were to remain under weather conditions during the summer months, it was thought that the beating rains and activities of soil organisms would be sufficient to cover them. The cultures were placed on the University Farm in such a position that they received full sunlight at the beginning of the period of exposure. During the summer, however, grass grew around the cultures so that for the latter part of the season they were somewhat protected from the sun. Unfortunately, the author was not able to keep records of the soil temperature during the experiment, or to make examination of the ova at desired intervals. Examination of the ova on October 13, 1928, showed that they had all disintegrated. Only 35 ova were recovered from the three cultures. The contents of these were hyaline, and many contained a large refractive bubble which filled much of the interior of the ovum. Brown (1928) reports finding bubbles of like nature in the ova of *Ascaris lumbricoides* which had broken down as a result of dessication.

A similar study was made during the summer of 1929. Soil cultures of sand and humus were prepared and exposed under three conditions of sunlight. One series was placed in full sunlight; another, in thin grass about 14 inches high, so that it received some shade; and a third, under a hedge where there was complete shade. Unsegmented ova were planted on the surface of these cultures on July 5. There occurred almost 2 inches of precipitation on July 6 that mixed the ova with the surface soil particles and gave conditions comparable with those in animal pens of dirt floors. Soil temperature records and relative humidity readings of the air above the cultures were taken in the early morning before the sun had shone on them and again at 1:30 p.m., which is perhaps the hottest part of the day in this region. These data are recorded in Graph 4. The results of the examination of the ova at definite intervals are given in Table II.

Consideration of Table II, which gives the developmental stages of the ova at the intervals of examination, shows that in full sunlight none developed beyond the morula stage and that all were dead at the expiration of 11 days. Some of the ova exposed to full sunlight did reach the late morula stage but none in either the sand or humus culture developed so far as the vermiform stage. With some shade, the maximum number found in the motile embryo stage was 53.5 per cent. This was in the humus culture, as compared to only 18 per cent in the sand culture. In the shade cultures, 75 per cent of the ova in the humus soil were in the motile embryo stage when last examined, whereas in the sand soil, only 45 per cent were in this stage.

COMPARISON OF F_1 CROSSES WITH PROGENIES OF PARENTAL VARIETIES

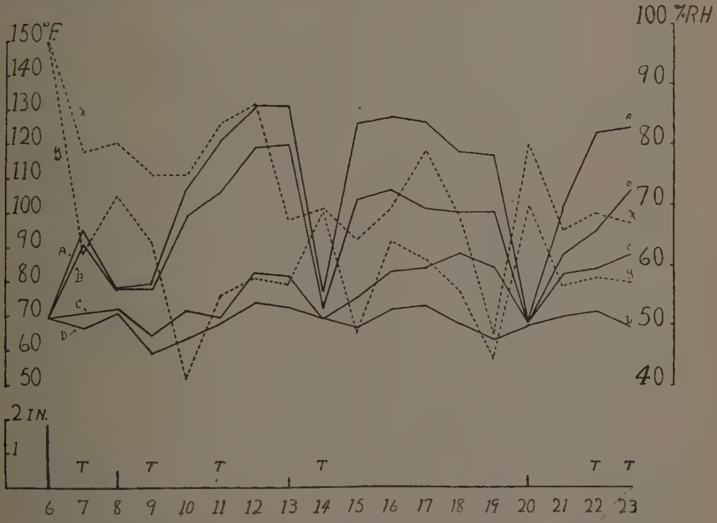
Cross	Vine growth ♀	Vine growth ♂	Vine growth F_1	Average yield lb. ♀	Average yield lb. ♂	Average yield lb. F_1	Inc. in yield over mean of parents per cent	Inc. in yield over highest parent per cent
. Acc. No. 7416	5.9	4.8	6.5	0.27	0.39	0.61	84.8	56.4
t Mountain	5.6	5.4	6.1	0.28	0.26	0.53	96.2	89.2
c. No. 7416	5.8	4.8	5.8	0.49	0.39	0.51	15.9	4.0
No. 7416	4.0	5.1	5.3	....	....	....	....	....
Acc. No. 7416	4.6	5.1	4.8	....	....	....	....	....
s	5.0	6.1	5.9	0.37	0.32	0.49	42.0	32.4
Acc. No 7416	5.0	...	4.6	0.37	....	0.39	....	5.4
untain	6.1	...	6.2	0.32	....	0.42	....	31.2
	5.5	4.6	6.7	0.36	0.46	0.55	34.1	19.5
	2.5	3.9	3.8	0.65	0.39	0.76	46.1	16.9
	4.4	3.0	4.3	1.03	0.39	0.61	—16.3	—68.8
	2.5	4.0	4.4	0.65	0.88	1.17	52.0	32.9
	2.0	4.0	4.0	0.20	0.88	1.15	112.9	30.6
5	2.0	3.0	4.0	0.20	0.66	0.69	60.4	4.5
5	3.0	3.0	4.6	0.39	0.66	1.21	125.7	83.8
						Average	50.3	31.5



Graph 3. Disintegration and Survival of Ova in Sand and Humus Soils Under Three Conditions of Sunlight from July 5 to July 19, 1929. Data taken from Table II.

Graph 3 gives a comparative picture of the number of ova disintegrating in the two types of soil under the three conditions of sunlight. In like manner, the survival of ova reaching the motile embryo stage under part shade is illustrated very vividly in the graph. The number of ova in this stage reached a maximum (18 per cent) in the sand culture on July 12 (7 days' exposure) then dropped to 5.5 per cent on July 16 (11 days' exposure). In the humus culture, the per cent developing to the coiled embryo stage reached a maximum (53.5 per cent) on July 16 (11 days' exposure), then dropped to 30 per cent on July 19 (14 days' exposure). Observations on the ova under complete shade were not carried far enough to designate the exact time at which the greatest number were in the coiled embryo stage. However, by looking at Table II, it is evident that the percentages found in that stage on July 19 (14 days' exposure), were very close to a maximum. From the data given in Graph 3 on disintegration and survival under part shade, it is possible to compute the percentage of ova disintegrating in the two types of soil before reaching the coiled embryo stage. This number is arrived at by subtracting the percentage of ova disintegrating after reaching the coiled embryo stage from the final disintegration figure. In the sand culture, 90 per cent — (18—5) = 77 per cent, the approximate number disintegrating before reaching the coiled embryo stage. In the humus culture, 57.5 per cent — (53.5—30) = 34 per cent, the approximate number disintegrating before reaching the coiled embryo stage. It is evident, from the data in Graph 3, that disintegration was much more rapid in sand soil than in humus under both part shade and complete shade. In full sunlight under the conditions of this experiment, the rate of disintegration was approximately the same in both types of soil.

Graph 4 gives the soil temperature records and relative humidity readings under the three conditions of sunlight during the experiment. The variation in relative humidity was so small under the three conditions that the complete series of readings has been combined into one graph. It should be remembered, however, that this graph does not give the relative humidity of the air among the soil particles on the surface, when the temperature at this level is higher than that of the air above. No measurement of the intensity of the light was made. However, by comparing the surface-soil temperature records, it is evident that there was a gradient in respect to the amount of light received under the different conditions. The highest recorded soil temperature in full sunlight was 131.9° F. (55.5° C.), whereas the highest temperature in part shade was 119.3° F. (48.5° C.). In complete shade, the temperature did not go above 84.2° F. (29.0° C.). The difference between sand and humus soil under like conditions was never more than a few degrees. The data given in Graph 4 indicate that high temperature alone, when considered separately from the dessicating effect of heat combined with dryness, was a factor in the destruction of ova under



Graph 4. Soil Temperature, Relative Humidity (Taken at a Level Two Feet Above the Soil), and Precipitation from July 6 to July 23, 1929. Data Recorded at Minneapolis, Minnesota

Explanation: A, maximum soil temperature in full sunlight; B, maximum soil temperature in part shade; C, maximum soil temperature in complete shade; D, minimum soil temperature; X, maximum relative humidity; Y, minimum relative humidity. Precipitation expressed in inches. T, traces of preciptation.

conditions of full sunlight. This is reasonable, as the surface-soil temperature in full sunlight on two consecutive days reached 131.9° F. (55.5° C.). This reading, it should be remembered, is not taken from a constant temperature record throughout the day. Thus it is very probable that this figure is not the highest that could be obtained for maximum soil temperature under these conditions.

In Kentucky

In the latter part of July and in August of 1928 an experiment was carried out in the western part of Kentucky to get data on the development and survival of ova under summer conditions in that region. Cultures, in series of two, were prepared from sand, clay, and humus soil, and exposed under two conditions of sunlight. One series received full sunlight and the other was located in the shade of a walnut tree. Unsegmented ova were placed on the surface of these cultures on July 23, 1928. In order to duplicate conditions found in a fresh stool of an animal, these cultures were moistened at the time the ova were planted. The surface of the soil in the series receiving full sunlight became dry with one day of exposure, whereas the cultures in the shade remained moist for many days.

Examination of the ova in the series exposed to full sunlight on August 6 (14 days' exposure), showed that they were all dead. Many of these contained the large bubble which was found in disintegrated ova after being exposed to summer conditions in Minnesota. The ova exposed in cultures under shade conditions were examined at intervals as indicated in Table III.

TABLE III

DEVELOPMENT SHOWN BY THE OVA OF *Toxocara canis* IN CULTURES UNDER SHADE CONDITIONS—EXPERIMENT STARTED JULY 23, 1928

Culture	Date examined	No. counted	Undeveloped	Morula	Vermiform	Motile embryos	Dead
			per cent	per cent	per cent	per cent	per cent
Sand.........	Aug. 13	200	1.0	1.5	0.0	90.0	7.5
Sand.........	Sept. 3	100	0.0	1.0	0.0	93.0	6.0
Clay.........	Aug. 13	200	3.5	0.0	0.0	90.0	6.5
Clay.........	Sept. 3	100	0.0	0.0	0.0	94.0	6.0
Humus.......	Aug. 13	65*	4.6	0.0	0.0	86.6	8.8
Humus.......	Sept. 3	†					

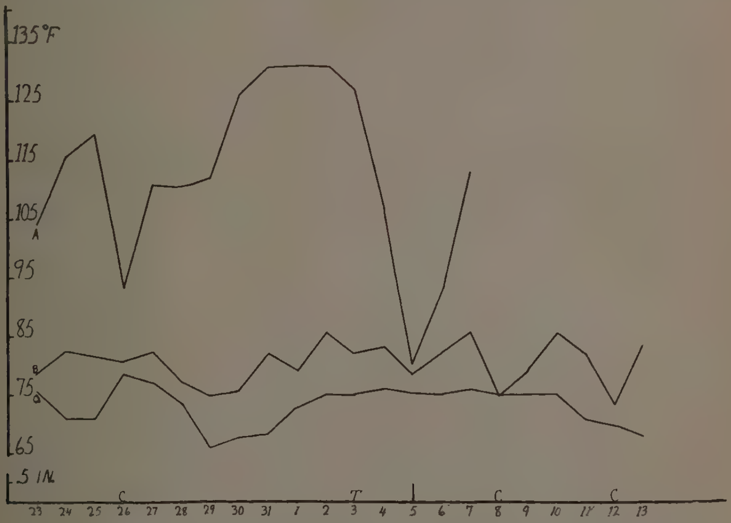
* This figure represents the total number of ova recovered from the entire culture. An error in the original number planted perhaps accounts for this result.

† No examination.

The data given in Table III indicate that the amount of disintegration did not increase in sand and clay soil from August 13 (21 days' exposure) to September 3 (42 days' exposure). During this period the number in the coiled embryo stage increased a little, as is shown by the records from sand and clay cultures.

Graph 5 indicates the physical data recorded along with this experiment. The great contrast between the surface-soil temperature in shade and in full sunlight is again seen here. In full sunlight, the highest recorded soil temperature was 131.9° F. (55.5° C.), whereas the highest temperature found in the shade cultures was 87.8° F. (31.0° C.).

That ova in the series exposed to full sunlight should disintegrate with 14 days' exposure in the soil is not surprising, as the temperature on three consecutive days reached 131.9° F. (55.5° C.). Here, as was found under like conditions in Minnesota, the surface-soil temperature reached the absolute maximum or lethal point for the ova of this species. Examination of these ova at an earlier date would have given more accurate information on the actual time they will survive under the conditions here tested, but it was impossible to make such an observation.



Graph 5. Soil Temperature and Precipitation from July 23 to August 13, 1928
Data Recorded in Western Kentucky

Explanation: A, maximum soil temperature in full sunlight; B, maximum soil temperature in shade; O, minimum soil temperature. Precipitation given in inches. C, cloudy days. T, traces of precipitation. All data recorded at site of cultures.

Longevity in the Soil

The results of a single experiment on the longevity of the ova of *Toxocara canis* in the soil in the region of Minneapolis, Minnesota, are as follows. On November 27, 1927, ova in an unsegmented state were planted in a culture of humus soil and mixed with the upper half-inch soil stratum of the same. A soil sample of this culture was brought into the laboratory on February 4, 1928, and placed in an incubator that was kept at 25° C. On February 18, the ova were recovered and differential counts made. The results of this examination are given in Table IV, which shows that 84.5 per cent contained motile embryos and only 2.5 per cent had disintegrated.

TABLE IV

DEVELOPMENT OF THE OVA OF *Toxocara canis* AFTER BEING IN THE SOIL FROM NOVEMBER 24, 1927 TO FEBRUARY 4, 1928

	Undeveloped	Morula	Vermiform	Motile	Embryos	Dead
	per cent	per cent	per cent	per cent	per cent	per cent
200................	11.0	1.5	0.5	84.5	...	2.5

The ova in this experiment were not examined again until November 24, 1928, which was one year from the date they were placed in the soil. In this examination, a total of 55 ova were recovered from the entire culture. Of this number, 22 were hyaline, 22 contained a large bubble, and in 11 the outlines of the embryos were visible but disintegration was in progress.

This culture was located close enough to the thermocouple that Graph 1 expresses the physical condition of the environment during the winter months. The culture received full sunlight during the early summer but was protected from the heat by grass during the hottest part of the summer. The fact that the embryos in some of these ova had not completely degenerated when last examined, suggests that the ova of *Toxocara canis,* covered with surface soil to the depth that these were, may survive the summer months or even for one year under the conditions of this experiment in Minnesota.

DEVELOPMENT AND VIABILITY AT LOW TEMPERATURES UNDER LABORATORY CONDITIONS

In this study the ova were collected from the uteri of gravid females and kept in a 2 per cent formalin solution as a culture medium. The cultures were exposed in low temperature cabinets for varying lengths of time, as indicated in the summary of these studies given in Table V.

Ova from cultures numbers 7 and 8 were fed to young laboratory rats to determine whether they were capable of infecting an animal after being exposed to the temperature given in Table V. No migrating larvae were recovered from the organs of these test animals. This fact, with the further observation that these larvae disintegrated after an elapse of one week, indicates that —25.6° F. is fatal to infective ova of this species. The data in Table V indicate that 53.6° F. is very close to the minimum effective temperature for unsegmented ova, as no development occurred here during a period of 35 days. On the other hand, ova exposed at 62.0° F. for the same length of time, developed to the coiled embryo stage. The data obtained in these experiments compare very favorably with similar studies made by Cram (1924) on the ova of *Ascaris lumbricoides.*

TABLE V

Summary of Studies on Development and Viability of the Ova of *Toxocara canis* at Low Temperatures Under Laboratory Conditions

Condition of ova	Temperature	Period of exposure	Condition of ova	Result when cultured at 77.0° F.
1. Unsegmented	Constant at 62.0° F.	35 days	35 per cent motile embryos	Normal development
2. Unsegmented	Constant at 53.6° F.	35 days	No development	Normal development
3. Unsegmented	5 to —31.0° F.	7 days	No development	No development
4. Unsegmented	Alternated between 77.0° F. and 5.0 to —31° F.	3 days at each temp. for 15 days	No development	Died in 16-cell stage
5. Motile embryos	Constant at —13.0° F.	8 hours	Motile	Motile
6. Motile embryos	Constant at —13.0° F.	24 hours	Motile	Motile
7. Motile embryos	Constant at —25.6° F.	8 hours	Very little movement	Disintegrated in 7 days
8. Motile embryos	Constant at —25.6° F.	30 hours	None motile	Disintegrated in 7 days

DEVELOPMENT AND VIABILITY IN AIR OF KNOWN MOISTURE CONTENT

The data given in this report, on development and viability in air of known moisture content, are preliminary to further studies by the author on the moisture requirements of the ova of *Toxocara canis.* The moisture content of the air in these experiments was controlled by the chemical method. During the period of exposure the ova were in small, open vials 1 inch deep, over which air of the desired moisture content circulated. A summary of these studies is given in Table VI.

From the data given in Table VI, it is obvious that loss of water retards development. This corroborates the results of Otto (1929) on culturing the ova of different ascarids in air of known moisture content. Unless dessication is complete, development is resumed if the ova are returned to a water medium. This fact is illustrated by the figures on development at 52 per cent relative humidity. In air of 52 per cent relative humidity for a period of 7 days, the limit of development was the morula stage, with 87 per cent in this condition. These ova were then returned to a water medium, under which condition 78 per cent developed to the coiled embryo stage. In air of 52 per cent relative humidity, for a period of 11 days, 92 per cent of the ova were in the morula stage, but when transferred to a water medium only 4 per cent developed to the coiled embryo stage. At a temperature of from 27° to 30° C., the minimum requirement for ova to develop to the

TABLE VI

Development and Viability Shown by the Ova of *Toxocara canis* When Cultured in Air of Various Percentages of Relative Humidity*

A

Ova in unsegmented stage when exposed to humidified air

Days exposure	Relative humidity	Maximum development in humidified air	Motile	Disintegrated	Development when returned to water medium
	per cent		per cent	per cent	
3	0.0	7% early morula	...	89.0	No development
7	0.0	None	...	100.0	No development
3	31.0	17% morula	...	3.0	Continued development
7	31.0	20% morula	...	67.0	No development
7	52.0	87% morula	...	8.0	78% dev. to coiled embryos
11	52.0	92% morula	...	5.0	4% dev. to coiled embryos
20	52.0	....	...	100.0	No development
8	58.3	1.5% vermiform	...	23.5	No observations made
16	58.3	Morula (no count made)	...	(?)	8% dev. to coiled embryos
8	70.4	4% vermiform	...	4.0	80% dev. to coiled embryos
16	70.4	Morula (no count made)	...	(?)	30% dev. to coiled embryos
7	75.0	7.5% coiled embryos	7.5	4.0	77% dev. to coiled embryos
20	75.0	81% coiled embryos	3.0	14.0	Larvae freed from shell in contact with water 64% motile
7	nearly saturated	84.5% coiled embryos	84.5	0.0	

B

Ova cultured to motile embryo stage previous to exposure

Days exposure	Relative humidity	Per cent motile after exposure	Per cent disintegrated	Per cent of larvae motile when freed in water
1	0.0	80.0	7.0	
2	0.0	66.0	32.0	
7	31.0	0.0		20.0
20	52.0	0.0		1.0
20	75.0	57.0	38.0	
20	nearly saturated	83.7	2.5	

* The temperature ranged during the period of exposure from 27 to 30° C.

coiled embryo stage is a relative humidity of from 70 to 75 per cent. At 70.4 per cent relative humidity, for a period of 16 days, no ova were found beyond the morula stage, and when ova from this culture were returned to a water medium, only 30 per cent developed to the coiled embryo stage. This indicates that they were dying very rapidly under these conditions. At 75 per cent relative humidity, for a period of 20 days, 81 per cent of the ova had reached the coiled embryo stage and only 14 per cent had disintegrated. In air nearly saturated with moisture, 84.5 per cent of the ova developed to the coiled embryo stage in 7 days, which is just as rapid and within the range of the percentage which reach this stage when cultured in water or 2 per cent formalin. The maximum number of ova that undergo development when taken from the uteri of females, as these were, is from 85 to 95 per cent. A point of practical interest found in these studies is that lack of motility under the warm-stage microscope is not a sure test of whether the larvae are alive. This fact is illustrated by the ova cultured for 20 days at 75 per cent relative humidity. Under these conditions 81 per cent were in the coiled embryo stage, but only 3 per cent showed motility under the warm stage microscope. Yet when freed from the shell and in contact with water, 64 per cent of the larvae were motile. There is some indication that ova in the coiled embryo stage have a greater resistance to dessication than when in the various stages of development. For example, 31 per cent relative humidity for a period of 7 days was lethal to developing ova, but with ova containing coiled embryos when exposed to the same conditions for the same length of time 20 per cent of the larvae were definitely alive.

GENERAL DISCUSSION

Survival of Ova Under Winter and Summer Conditions

These studies clearly showed that from 75 to 80 per cent of the ova of *Toxocara canis* can, in the unsegmented state, survive the winter months in the soil under weather conditions in the region of Minneapolis. This apparent resistance to very low temperatures is accounted for by the fact that the surface-soil temperature under the protection of heavy snows is always much higher than the air temperature. This fact does not exclude the possibility, however, that extremely low temperatures may occur at a time when there is no snow on the ground. Inasmuch as laboratory tests indicate the ova of this species are killed at —25° F., there is always the chance that under certain conditions this temperature may be reached on the surface of the soil. However, records for two successive winters show that the lowest temperature recorded on the soil surface was 6.26° F. (—14.33° C.).

Observations on ova containing motile embryos, which were exposed to —13° F. (—25° C.) under laboratory conditions, demonstrate that they are relatively unaffected by this temperature. Thus it is safe to conclude that ova containing motile embryos would have survived under field conditions during the winter months equally as well as those in an unsegmented condition.

Under conditions of low temperature, the ova of this species may remain dormant in the soil for more than five months and then resume development if the temperature is raised above that of the minimum effective point. Ova having remained dormant for this period are not greatly reduced in vitality, as is seen by the large number that developed motile larvae. The larvae developed from these ova are capable of infecting an animal, as was shown by the test on a young laboratory rat.

The evidence derived from the studies reported here on the survival of the ova of *Toxocara canis* in the soil during the summer months corroborates the conclusions of Brown (1928), Caldwell and Caldwell (1928), and Otto (1929) that dessication is the greatest lethal factor to development and viability of ascarid ova under field conditions. An additional point brought out in the present studies is the fact that the surface-soil temperature in full sunlight may, during the hottest part of the summer, reach the absolute maximum temperature for ascarid ova (55.5° C.), as indicated by the records from both Kentucky and Minnesota.

Relation of Various Physical Factors to Dessication of Ova

The question of the relative suitability of different soil types for development and survival of ascarid ova under field conditions and the relation this bears to incidence and distribution, has been given considerable attention by recent investigators. Brown (1927), working at Penonome, Panama, found that the ova of *Ascaris lumbricoides* in sand cultures exposed to full sunlight disintegrated before reaching the coiled embryo stage, whereas from 85 to 90 per cent of those in clay, loam, and humus soil cultures, under like conditions became embryonated. Otto (1929) reports that in southwestern Virginia *Ascaris* ova exposed to sunlight in a mixture of cinders and loam were never more than 3 per cent embryonated. In sand and loam soils, 36 and 38 per cent and in clay a maximum of 73 per cent developed to the coiled embryo stage. Under shade conditions the maximum number found in the embryonated stage was about the same in all four types of soil, varying from 73 per cent in sand to 89 per cent in clay. In a laboratory experiment in which he passed air of different relative humidities over soil cultures of sand, loam, clay, and humus which had been previously oven dried, it was found that ova in sand and humus in air of 70 to 75 per cent relative humidity developed to the coiled embryo stage, but in air of from 40 to 50 per cent relative humidity, the ova disintegrated in all the soils before becoming embryonated. In the same experiment he used air saturated with moisture and found no difference in the number becoming embryonated in the different types of soil. At the end of the experiment, it was found that the sand had taken up less moisture in saturated air than the other soils did in air either 40 to 50 per cent saturated or 70 to 75 per cent saturated. Altho the sand contained less moisture by weight in air of 70 to 75 per cent relative humidity than the other soils did at a relative humidity of 40 to 50 per cent, ova became embryonated in sand at 70 to 75 per cent relative humidity and disintegrated in all the soil cultures at 40 to 50 per cent relative humidity. In a previous test, he had shown that ova could become embryonated in air of from 70 to 75 per cent saturated with moisture. From these data he states that "Under identical conditions of temperature and atmospheric moisture one soil apparently makes as good a cultural media as another. . . . It is at once evident that the relative soil moisture does not affect the suitability of these soils for culturing ascarid eggs."

The results of the above experiment are what might have been expected, but do not justify the interpretation placed upon them by Otto. A fundamental principle overlooked by the investigator is that the moisture content of the air and the soil moisture at the surface tend to reach a state of equilibrium. Evaporation of moisture from the soil and the removal of moisture from the air by the soil are processes resulting from this principle. It is very evident that the ova on the surface of the sand culture, in air of from 70 to 75 per cent relative humidity, were not dependent upon soil moisture to prevent dessication. For in this test, the conditions were such that this state of equilibrium could be reached between the moisture content of the air among the soil particles on and near the surface and the air above the culture. The relative suitability of different soils as culture media for ascarid ova, as shall be discussed later, is dependent upon the texture and composition of the soils, which in turn determines the rate of evaporation, under like conditions, moisture capacity, and like characteristics.

In the present studies, ova in sand, clay, and humus soils exposed to full sunlight during the hottest part of the summer in both Kentucky and Minnesota disintegrated before developing to the coiled embryo stage. It is not clear in these experiments whether it was a combination of high temperature and lack of moisture or high temperature alone that killed the ova, as in both tests the surface soil temperature reached 131.9° F. (55.5° C.) before they were examined. Under part shade conditions in Minnesota, a maximum of 18 per cent reached the coiled embryo stage in sand, as compared with 53.5 per cent in humus. After 14 days' exposure under these conditions, only 5 per cent were left in the embryonated stage in sand in contrast to 30 per cent in humus. In this test the sand was observed to dry out more quickly than the humus, and likewise the temperature in the sand culture on three days during the first week of exposure was 5 degrees higher than in the humus. In the shade cultures in Minnesota, where the temperature was the same in both cultures but remained relatively low, development was retarded. When these ova were last examined, 75 per cent in the humus soil were embryonated and 17.5 per cent disintegrated as compared with 45 per cent embryonated and 42.5 per cent dead in the sand. In cultures of sand, clay, and humus under full shade in Kentucky, the number becoming embryonated was approximately the same in each soil type (85 to 90 per cent) and observations on ova in sand and clay cultures indicate that no disintegration occurred with 42 days' exposure during the latter part of July and the month of August.

The explanation for the higher disintegration of ova in sand as contrasted with humus soil under both part shade and complete shade in Minnesota is to be found in the nature of the soil in which they were exposed and other physical forces present during the period of exposure. The *rate* of evaporation of moisture from the soil is regulated by temperature, relative humidity, wind velocity, and size of soil particles, which determines the water-binding capacity, compactness, etc. The free water in the soil (hygroscopic not included) available for organisms is determined by the chemical nature of the soil and size of soil particles. Humus soils ordinarily contain more available moisture for organisms than do clay, sand, and others. Under field conditions, apart from very exceptional cases, evaporation from sand is more rapid than from clay and humus soils. As the soil becomes dry, the temperature rises, which in turn increases evaporation, if humidity conditions permit. In the cultures under part shade, when the soil temperature ranged from 100 to 119° F., evaporation was rapid. However, the rate of evaporation was greater from the sand than from the humus because of the larger air spaces between the sand particles, which permit better aeration at the surface. In complete shade the physical conditions were the same except for the lower surface-soil temperature, which was never more than 84.2° F. Here the rate of evaporation was slower and the disintegration of ova less than in part shade, but higher in sand than in humus soil. How then can the lack of disintegration of ova in sand and clay soils after 42 days' exposure in the shade in western Kentucky be explained? The answer to this question is that the physical factors involved in the shade experiment in Kentucky were not the same as in a similar test in Minnesota. A striking difference is the greater average wind velocity in Minnesota which would increase the rate of evaporation in cultures that were otherwise subjected to the same conditions. From this discussion it is obvious that the death of ascarid ova from dessication under field conditions is the result of the combined effect of a series of interdependent physical factors, of which soil type is one of the most important.

The results of laboratory tests on culturing the ova of *Toxocara canis* in air of different relative humidities indicate that they are relatively resistant to dessication. The data obtained in these tests suggest three important points which have bearing on the development and survival of the ova of this species under field conditions: (1) The water content of an egg at the time it is discharged does not have to be maintained during the developmental period. (2) The loss of water by evaporation up to a certain amount has no apparent harmful effects, but beyond this point ova die rapidly. (3) Ova are retarded in development by loss of water, but unless they die of dessication, they continue development when given moisture. The slow rate of evaporation combined with this faculty of remaining alive when partly dessicated probably accounts for field observations that ova remain viable in apparently dry soil for many days. If this interpretation is correct, the amount of water lost through evaporation and the chances of coming in contact with available soil moisture are determined by the nature of the soil and the other physical factors during the period of exposure. It follows, then, that the ratio between loss and gain of water by ova is determined by the behavior of a natural physical system which varies in its effects as any one of the physical factors involved varies.

SUMMARY AND CONCLUSIONS

The ova of *Toxocara canis* survived the winter months under weather conditions during the season of 1927 and 1928 in the region of Minneapolis, Minnesota.

Observations during two consecutive winter seasons indicate that the surface-soil temperature did not go low enough to kill the ova of this species, altho air temperature was as low as —24° F. (—31.11° C.).

The great contrast between air temperature and soil temperature during the winter season is accounted for by the abundance of snow, which acts as a blanket and keeps the surface soil relatively warm.

Fur farmers can not rely upon having the soil temperature of animal pens in which snow is allowed to acccumulate, go low enough to kill the ova of this roundworm.

Surface-soil temperature of 131.9 degrees F. (55.5° C.) were obtained in Kentucky and Minnesota on plots which had no protection from the sun. In cultures under these conditions, ova disintegrated before reaching the infective stage.

Disintegration of ova was greater in sand than in humus soil both in part shade and complete shade during the summer in Minnesota.

In Kentucky no apparent disintegration occurred in clay and sand soil with 42 days' exposure in complete shade during the latter part of July and the month of August.

Laboratory tests indicate that, at a temperature of from 27° to 30° C., a relative humidity of 75 per cent is the lowest in which the ova of this species will complete development.

It is not probable that ascarid ova can utilize atmospheric moisture before it is precipitated. Thus, retardation of development in air which is less than saturated with moisture is caused by loss of water from the ova. When this loss of water is great enough, death from dessication results.

Disintegration of ova in the soil from dessication is the result of the combined effects of a series of interdependent physical factors of which soil type can not be excluded.

PRACTICAL APPLICATION

Recommendations in regard to the reduction of soil infections of ascarid worms, based upon the data given in this report, can only be of a prophylactic nature. It is true here as in any such measure, that the efficiency of the method is determined by how rigidly one adheres to it. Laboratory tests show that the ova of *Toxocara canis* do not undergo development at a temperature under 50° F. Thus, if animal pens are cleaned of all excrement in the late fall, animals are relatively safe from new infections during the winter months, because ova deposited within this period do not develop until the temperature rises the following spring. This practice of thoroly cleaning pens of the remains of broken down animal stools in the late fall, or removing animals at this time to pens which are known not to have infective ova on the floors, should greatly reduce new infections during the winter season. It is true, however, that all ova can not be eliminated from pens that have dirt floors by removing the remains of excrement, as many eggs become mixed with the surface soil. If snow is removed from the pens during the winter months instead of being allowed to accumulate as is the usual practice, there is a very good chance that ova on the floors will be killed by the extremely low temperatures of our northern states. Laboratory tests indicate that the ova of this species are killed at —25° F. The data in this report clearly demonstrate that this temperature will not be attained on the floors of animal pens if they are covered with snow.

An effective recommendation for the reduction of new infections during the summer, and perhaps for a complete sterilization of the soil of all ova near the surface, is to provide sufficient sunlight in animal pens during the summer months. Observations on the longevity of the ova of *Toxocara canis* on the surface of the soil, when exposed to different amounts of sunlight during the summer months, support the validity of this recommendation. It is a general practice among breeders to have pens in the shade. This provides ideal conditions for almost all the ova to develop to the infective stage, and to remain viable for long periods. The present status of these studies indicates that the provision for full sunlight in animal pens during the summer months is one of the most effective means of destroying ascarid ova that are present. This applies to pens that have wood floors as well as to those in which the soil serves as a floor.

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Minnesota Agricultural Indexes of Prices, Quantities, and Cash Incomes
1910-1927

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CONTENTS

Page

Summary 3

Introduction 5
  Need of an index of Minnesota farm prices 5

Method of construction of the price index 6
  Products included 6
  Period chosen for base 6
  System of weighting used 8

Price index series for all commodities combined 11

Price indexes for three major groups of products 14

Quantity index for all commodities marketed 15

Index of gross cash income 19

Gross cash income in dollars 20

Sources of price and quantity data and methods of estimating amounts marketed 30
  Wheat 30
  Corn 34
  Oats 38
  Barley 41
  Rye 45
  Flax 48
  Hay 51
  Potatoes 55
  Hogs 60
  Cattle and calves 64
  Lambs-sheep 70
  Chickens 73
  Eggs 77
  Butterfat 81
  Milk 85

MINNESOTA AGRICULTURAL INDEXES OF PRICES, QUANTITIES, AND CASH INCOMES, 1910-1927

Albert G. Black[1] and Dorothea D. Kittredge

SUMMARY

An agricultural price index series is needed which includes only the products sold by Minnesota farmers and excludes such products as cotton, cottonseed, tobacco, and fruits. The inclusion of such products as specified invalidates, for use in Minnesota, the price index of the United States Department of Agriculture.

Monthly and yearly price indexes, therefore, have been constructed, in which price changes from 1910 to date, of the sixteen principal agricultural products of Minnesota—wheat, corn, oats, barley, rye, flax, hay, potatoes, hogs, cattle, calves, lambs-sheep, chickens, eggs, butterfat, and milk—have been measured from average prices in the corresponding period of 1924-25-26. The annual indexes are based on an average for the years of this period and the monthly indexes on an average of the corresponding months in the years 1924-25-26. A formula of the type known as Fisher's "ideal" has been used in the construction of the index. This provides for a weighting of price changes by a combination of the quantities sold in both the current month and the corresponding month of the base period, which approaches more closely the conditions of economic reality than weighting by quantities of either base or current period alone. Constant "normal" weights of any kind are objectionable, especially in agriculture, where, because of shifts in production, bumper crops, and crop failures, current marketings are likely to vary widely from those represented by a base period normal. Under these circumstances, constant normal weights cause erroneous weighting of prices. Neither does a constant monthly percentage of the crop sold furnish a reliable weighting for prices within a year.

The Minnesota farm price index for 1911 showed the lowest average for the period from 1910 to 1927. A pronounced rise occurred during 1916, 1917, 1918, and 1919. The 1919 yearly index was the highest of the series. The maximum point for any monthly index was reached in April, 1920, and was followed by a sharp decline, the low point of which was reached in December, 1921. After a period of low prices in 1922, 1923, and the early part of 1924, the index rose to a somewhat higher level, which was maintained generally until the decline

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[1] Resigned August 1, 1929.

in the latter months of 1927. Price indexes for groups of products—livestock, crops, and dairy and poultry—have been constructed for months and years by the same methods as those used for the price index of the entire sixteen commodities. An examination of these three major groups suggests somewhat different characteristics of price behavior both among the groups themselves and between periods of rising and falling prices.

In order to ascertain the changes in volume of agricultural products marketed by Minnesota farmers, an index series of quantities also has been constructed. The methods used in the construction of the quantity index have been identical with, or analagous to, those used in making the price index. The index of quantities sold revealed a surprising trend in production. The index was lowest in 1911. From 1911 to the beginning of 1919 the trend was generally upward, except for slight recessions in 1914, 1916, and the early part of 1917. The quantity of marketings declined in 1919 and 1920, but that period was followed by four years in which a decided upward trend was evident. The high point was reached in October, 1924, after which time there was a gradual downward trend in the quantity index to the end of 1927. The general upward trend in farm marketings for the period as a whole represents conditions in Minnesota probably not duplicated in many other sections of the country. Much of the increase resulted from an increase in livestock, livestock products, and corn. The products which constituted the bulk of farm production in the early part of the period have either decreased or increased slightly. Not many states have experienced such rapid changes in types of commodities produced as have taken place in Minnesota.

An index series of gross cash income for Minnesota has also been constructed. When formulas of the type of Fisher's "ideal" are employed for the price and quantity indexes, i.e., formulas which meet the factor reversal test, the product of the two indexes will result in the index of gross cash income.

The construction of these three series indicates that the quantity of farm production in Minnesota has been exerting a greater effect upon farm incomes than has been recognized. Particularly was this true in the period 1921 to 1924, when the index of gross farm income rose because of a combination of a low price index and a steadily increasing quantity index.

The total amount in dollars received from the sales of the sixteen principal farm products may be considered as the gross cash income, if it is kept in mind that only sixteen major products are included, and that on account of insufficient data several quantities have had to be estimated by a variety of methods. The percentages contributed to the gross annual income by individual products show that wheat as a predominant source of cash income in the earlier years of the period has been replaced by butterfat and hogs in the later years.

INTRODUCTION

Need for an Index of Minnesota Farm Prices

Until the Minnesota farm price index series was prepared, the only measure of agricultural prices available for use in analyzing local price situations was that constructed for the United States as a whole by the Bureau of Agricultural Economics of the United States Department of Agriculture. The inadequacy of such an index to represent the agricultural price level of Minnesota lies chiefly in the fact that it includes price changes of cotton and cottonseed as a relatively important item, and those of tobacco and citrus fruits as less important. In the months when the price of cotton moved in the opposite direction from the price of the majority of other agricultural products, this index was especially unreliable as an indicator of the Minnesota farm price level. Figure 1 shows the price indexes for the United States as a whole, cotton and cottonseed, and the approximate index of Minnesota farm products, for the period 1922-27. The Minnesota figures used in this graph have been adjusted as far as possible with respect to base period and formula to conform to those of the Bureau of Agricultural Economics, and differ to that extent from the regular Minnesota series, which appears later in this bulletin. The graph shows clearly that the index of the United States Department of Agriculture for all groups of agricultural commodities was too high to represent the Minnesota price level for practically all the months from 1922 to 1925, and that from 1926 to the fall of 1927 the United States index was consistently below the Minnesota price level. A number of factors may have operated to bring this about, but the trend of prices of cotton and cottonseed, as shown on the graph, seems sufficient in itself to account for the differences. The index for the United States as a whole must include, of necessity, the prices of cotton and cottonseed, but when situations such as those from 1922 to 1927 prevail, error and possible injustice result in assuming that the Minnesota agricultural price level is represented by the price index of all groups of agricultural products produced in the United States. The only practical remedy is for each state and possibly for certain sub-divisions of a state to have individual price indexes. Such indexes can then include only the prices of the agricultural commodities actually grown in the area, in the degree of importance which the marketings of each product warrant. The price index for the whole state of Minnesota does not represent the price situation of all sections as satisfactorily as would be possible if the state were divided into five or six geographical sub-divisions and separate price indexes were constructed for each district—a project which is now under way.

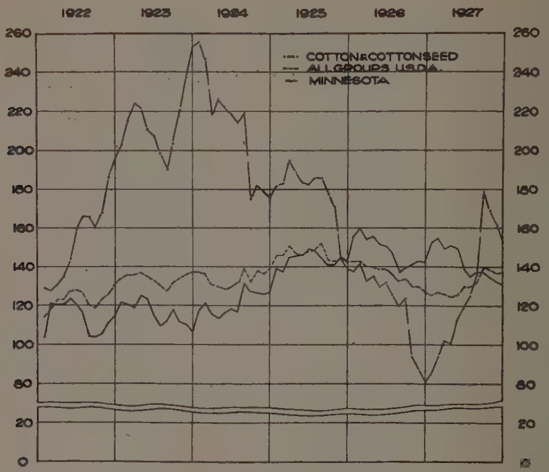

Fig. 1. Price Indexes of All Groups of Agricultural Commodities in the United States, Cotton and Cottonseed, and Minnesota Farm Products, 1922-1927

The indexes for all groups, and cotton and cottonseed, are prepared by the United States Bureau of Agricultural Economics on a base of August, 1909 to July, 1914. The Minnesota index shown on this graph has been reduced to a simple aggregative type of index, and expressed on a base of 1910-1914, in order to make the comparison more nearly accurate. Several technical differences still remain in the construction of these indexes, so that the comparison is intended to be only approximate.

METHOD OF CONSTRUCTION OF THE PRICE INDEX

Products Included

The Minnesota price index represents price changes in the sixteen principal agricultural products marketed by the farmers of the state: wheat, corn, oats, barley, rye, flax, hay, potatoes, hogs, cattle, calves, lambs-sheep, chickens, eggs, butterfat, and milk. Indexes for the individual months as well as for each year have been computed for the period from January 1910 to date.

Period Chosen as Base

The annual price indexes for Minnesota have been measured from the average prices of these sixteen products in the years 1924-25-26. For the monthly indexes an average of the corresponding months of the years 1924-25-26 has been taken as a base. For example, an average of the prices in the three Januarys of these years serves as a base from which the price changes of other Januarys are measured. The same method of measurement applies to all other months. The measurement of price changes of any month in relation to the average price of the corresponding months of the base period provides for an elimination of seasonal fluctuations. Altho this does not insure a perfect elimination of seasonal fluctuations in the index number, it removes such fluctuations as were experienced in the years 1924-25-26. Furthermore, seasonal variations are eliminated from the index only so far as the fluctuations of these years were confined to season alone (i.e., did not include secular trend or irregular fluctuations of importance), and the elimination is valid only if the seasonal variations of these years were of a "normal" character. The seasonal elimination provided for in the index number, as based on corresponding months of 1924-25-26, has been analyzed carefully in order that a comparison may be made from time to time between it and the current series of prices to ascertain whether such an elimination of season continues to be warranted.

A broadened base of three years has been selected because agricultural production is somewhat subject to variation beyond the control of those engaged in the industry, and conditions in a single year may not be truly representative. A price index of agricultural products based upon an average of a period of years is a safer guide than one based upon a single year, particularly when the index is prepared for a single state. Local crop conditions may affect state production whereas conditions for the entire nation may be normal.

It seemed desirable to choose a base in the post-war period. If a pre-war base had been selected the latest year not affected by war conditions was 1913. Since that date there has been a tremendous economic upheaval. Conditions of production, likewise, have been seriously disturbed. New financial institutions have been established. Methods of distribution have been affected in certain lines by the development of co-operative marketing. In short, the economic world of today is vastly different from that of 1913. It is extremely difficult to look backward from the present and obtain any clear-cut picture of conditions as they were fifteen years ago. Too many things have happened in the meanwhile. Owing to the fact that we are living and producing under post-war conditions, it appeared logical to relegate the war and pre-war periods definitely to the past and select a base representative of present conditions.[2]

A further consideration in selecting the base period was the fact that price and quantity data are much more satisfactory for recent years than for the pre-war period. It was believed more advisable to adopt a base period for which data were accurate and easily available and to build back from this base into the period when data were less authentic and less plentiful, than to select a distant base and to build forward from it. The latter choice could not have produced reliable results.

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[2] The selection of a recent base period conforms to the practice followed by other institutions publishing index numbers. notably the Bureau of Labor Statistics, which has recently shifted the base of its index number of wholesale prices from 1913 to 1926; the Federal Reserve Board, which issues its new indexes of industrial production on a base of 1923-24-25; the National Bank of Commerce in New York, which uses 1923-24-25 as the base period for its wholesale price index.

System of Weighting Used

The prices entering into an index number must be weighted according to their importance, if the composite index is to represent adequately the existing price level. The only means of judging the importance of a price is by the amount of a commodity sold at that price. For the Minnesota index, a formula[3] has been employed which combines the weightings of the quantities sold in the base period with the quantities sold in the current period. This seems to be an especially desirable system of weighting for an index of agricultural prices. The alternative of this method is a system of weighting prices by constant quantity weights, either by the average in some base period or some other concept of normal. In some fields of index number construction, where changes occur gradually, no error of consequence is introduced by this method. In the field of agriculture, however, where quantities marketed vary widely, even between two consecutive years, because of crop failures, bumper crops, shifts in production, retarded or advanced seasons, and the like, constant weights throw an erroneous weighting upon prices in those periods when the actual marketings vary widely from the amounts represented in the "normal" or base period weightings. For example, if constant normal weights are used, a bumper crop which results in a reduced price per unit can not be given the influence in the index number that its importance demands. The resulting price index will show a price reduction smaller than the actual decrease. Similarly, a crop failure causes the price index to reflect a rise in prices which is unwarranted. The high price when constant weights are used is weighted by a larger quantity than that actually sold.

For illustrative purposes a case may be taken where there are only two commodity prices entering into the index number. The price of each in the base period is 50 cents per unit and the quantities marketed are 1,000 units. In the given period the price of commodity A increases to $1.00, the price of commodity B remaining the same. If constant

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[3] $$\sqrt{\frac{\Sigma[p_1 \quad q_{0(cm)}]}{\Sigma[p_{0(cm)} \quad q_{0(cm)}]} \times \frac{\Sigma[p_1 \quad q_1]}{\Sigma[p_{0(cm)} \quad q_1]}}$$

p_1 = price in current month.
q_1 = quantity marketed in current month.
$p_{0(cm)}$ = average price in corresponding months of 1924-25-26.
$q_{0(cm)}$ = average quantity marketed in corresponding months of 1924-25-26.

weights are used the price index will rise to 150.[4] In the case of agricultural products whose demand is almost unchanged over a period, variations in price are caused largely by fluctuations of supply. There is a normal inverse relationship between price and amount sold.[5] In the case cited this normal inverse relationship is ignored because it is assumed that the same quantity of commodity A was exchanged when the price rose to $1.00 as when the price was 50 cents. Obviously this is an erroneous assumption because the price of commodity A could not have increased 100 per cent if the quantity sold had remained constant. Therefore, if the quantities of products actually sold in the current period are not given consideration in an index, the resulting average must be incorrect because some prices will exert more influence than they should and others less than they should.

The change in wheat production in Minnesota offers a case in point. In 1913 the production was 68 million bushels and in 1926 it was 25 million bushels. Clearly, wheat was not so important in 1926 as in 1913. To weight its price by constant weights taken, let us say, in 1913 would give the wheat price an importance in the index for 1926 and others years of low production which it does not deserve.

Moreover, a reliable weighting for prices within the year is not furnished by a constant monthly "normal" percentage of the crop sold. In the case of potatoes, for example, different years show different tendencies on the part of farmers in marketing their crops. By January 1, 1917, the growers of Minnesota potatoes had sold 38 per cent of their crop, and on January 1 of the following year, only 20 per cent.[6] The monthly marketings of many agricultural products vary from year to year with the experience and circumstances of the previous season, the size of the crop, the current price, the price expected later in the year, and the judgment of farmers in general. Retarded and advanced seasons also cause variations in the monthly quantities sold in different years.

If the investigation of price fluctuations centers around mere price changes, without regard to the importance of the prices involved, there can be no objection to the use of constant weighting, or, for that matter, equal weighting. But if the object is to prepare an index which is to take account of the importance of the specific prices making up the price level, constant weighting does not serve the purpose. The economists who object to the introduction of current quantities into a price index number probably would not object to a quantity weighting which was an average of the quantity marketed in the base period and that marketed in the given period. Some highly desirable index numbers

[4] Computed from aggregative type of formula with base period weights.

[5] Russell C. Engberg, Industrial Prosperity and the Farmer. Appendix B., p. 279 ff.

[6] U.S.D.A. Yearbook 1922, p. 674.

have such a weighting.[7] The weighting embodied in the formula adopted for the Minnesota index is in essence a geometric mean of the base and given period quantities and is almost the same as the arithmetic mean of the two. This system of weighting takes account of decided changes in quantity between the base period and the current period, and thus gives a more accurate picture of the real changes in the price level than is possible when constant weights are used.

Furthermore, the Minnesota price index meets both the time reversal and the factor reversal tests that have been proposed by Prof. Irving Fisher[8] as the criterion of index number accuracy. The total value criterion[9] proposed by Prof. Fisher does not need to be applied to the Minnesota index, as this index is not based on a sample of prices and quantities but embraces, as nearly as data are available, the total commodity marketings of the farmers of Minnesota.

The principal objection to the use of a formula with the system of weighting used in the Minnesota index number is the difficulty and additional labor of securing current quantities for the weights. Without doubt, the work of compiling a price index is increased materially when the quantities sold in each current month are incorporated. It is a difficult but not impossible task, especially in recent years when data are recorded more completely than formerly. Moreover, when an index of income is also a consideration, as it was in Minnesota, quantities marketed currently are absolutely essential, and thus these additional data are available for weights in a price index if desired. There is, however, an unavoidable delay in securing these current quantities. Prices may be secured promptly but the quantity sold at the price will not be available until later, so that a final index of price by this formula can not be computed for some time after the close of the current month. It will be observed, however, that the first half of the Minnesota formula is an aggregative type with base period weights.[10] This can be computed currently and used as a preliminary index until the quantities necessary for the construction of the final index, are available. In approximately 80 per cent of the 216 months of the period from 1910 to 1927, these two indexes differed from one another by not more than three points—within a range from —1.5 to +1.5. In other months these indexes showed differences as large as +7 and —4, and a combination of unusual circumstances might result in still greater differences between the preliminary and final indexes. Notwithstanding these cases, no more satisfactory preliminary measure that can be issued currently has been found.

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[7] For example, Formula 2153, Fisher's Making of Index Numbers, p. 484.

[8] Irving Fisher, The Making of Index Numbers, Chapter IV.

[9] Irving Fisher, Journal of American Statistical Association, January, 1928.

[10] $\frac{\Sigma[p_1 \quad q_{0(cm)}]}{\Sigma[p_{0(cm)} \quad q_{0(cm)}]}$

PRICE INDEX SERIES FOR ALL COMMODITIES COMBINED

The index series of Minnesota farm prices, by months and years, is shown in the first column of Table 1. The index series in columns two and three are discussed in later sections of the bulletin. The monthly price indexes appear on the graph of Figure 2.

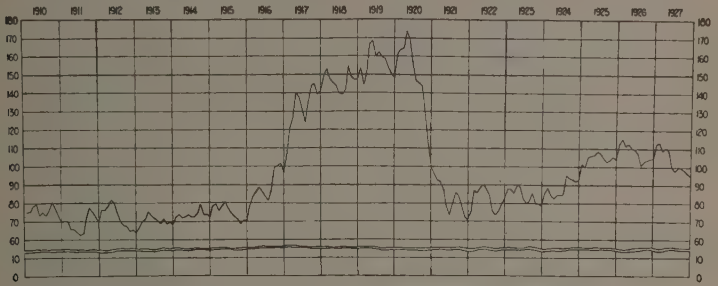

Fig. 2. Price Indexes of Minnesota Farm Products by Months, 1910-1927 (Average of corresponding months of 1924-25-26=100)

Table 1

Monthly and Yearly Indexes of (1) Prices and (2) Quantities Sold of Minnesota Farm Products, and (3) Gross Cash Incomes of Minnesota Farmers, 1910-1927

(Average of corresponding months of 1924-25-26=100.)

	Price	Quantity	Gross cash income
1910			
Average	75.7	58.0	43.9
January	75.1	59.5	44.7
February	75.5	61.7	46.6
March	78.6	59.4	46.7
April	79.6	48.7	38.8
May	73.2	53.4	39.1
June	75.0	53.7	40.3
July	73.4	51.4	37.7
August	76.0	61.1	46.4
September	80.7	65.2	53.3
October	77.6	59.3	46.0
November	73.2	57.9	42.4
December	68.9	59.1	40.7
1911			
Average	69.5	54.8	38.1
January	70.3	56.5	39.7
February	70.1	49.5	34.7
March	65.8	54.4	35.8
April	65.7	51.1	33.6
May	64.0	59.7	38.2
June	62.8	60.6	38.1
July	63.4	56.3	35.7
August	72.2	46.7	33.7
September	77.7	54.4	42.2
October	75.2	53.9	40.5
November	72.2	61.6	44.5
December	69.7	54.4	37.9
1912			
Average	70.9	60.6	43.0
January	76.1	52.9	40.0
February	76.3	55.0	42.0
March	78.2	55.4	43.3
April	81.8	48.9	40.0
May	80.1	54.2	43.4
June	74.5	52.9	39.4
July	69.9	46.9	32.8
August	67.8	60.9	41.3
September	67.3	65.5	44.1
October	64.5	72.6	46.8
November	65.1	78.8	51.3
December	63.9	73.6	47.0
1913			
Average	70.1	68.8	48.2
January	66.4	66.7	44.3
February	69.9	64.1	44.8
March	71.0	66.2	47.0
April	75.2	58.9	44.3
May	73.0	61.4	44.8
June	71.7	65.0	46.6
July	70.2	57.4	40.3
August	68.9	65.9	45.4
September	71.2	85.5	60.9
October	68.6	74.2	50.9
November	69.3	77.1	53.4
December	68.6	73.5	50.4

Table 1—Continued

	Price	Quantity	Gross cash income		Price	Quantity	Gross cash income
1914				1918			
Average	73.5	66.4	48.8	Average	146.9	81.1	119.2
January	72.1	68.9	49.7	January	149.2	69.4	103.6
February	73.6	68.6	50.4	February	153.2	68.3	104.6
March	71.9	69.5	50.0	March	147.9	75.8	112.1
April	72.3	61.0	44.1	April	145.4	70.4	102.3
May	73.5	61.6	45.3	May	144.0	77.3	111.3
June	72.2	62.9	45.4	June	139.9	74.9	104.8
July	72.5	58.9	42.7	July	139.3	63.7	88.7
August	74.3	61.6	45.8	August	141.4	94.3	133.3
September	79.2	71.5	56.6	September	154.7	94.1	145.5
October	73.4	69.2	50.8	October	148.7	95.0	141.3
November	73.9	69.9	51.0	November	147.1	80.8	118.8
December	72.4	67.7	49.0	December	147.7	95.5	141.0
1915				1919			
Average	74.0	71.9	53.2	Average	155.9	74.2	115.7
January	78.2	72.4	56.6	January	153.6	68.9	105.8
February	79.3	62.9	49.9	February	144.6	70.7	102.3
March	75.7	59.6	45.1	March	150.1	83.1	124.7
April	78.1	57.5	44.9	April	166.8	78.2	130.4
May	80.7	68.9	55.6	May	168.8	84.4	142.4
June	77.0	63.4	48.8	June	159.7	82.2	131.3
July	74.3	61.4	45.6	July	162.1	77.1	124.9
August	72.5	51.2	37.1	August	159.8	75.0	119.9
September	71.2	71.2	50.7	September	158.7	70.1	111.2
October	68.6	83.5	57.3	October	153.7	69.0	106.1
November	70.4	100.3	70.6	November	150.2	69.3	104.1
December	70.2	98.1	68.9	December	148.3	68.3	101.3
1916				1920			
Average	89.9	67.0	60.2	Average	144.9	69.2	100.3
January	78.1	67.5	52.7	January	160.4	72.5	116.3
February	83.8	76.7	64.3	February	163.5	66.5	108.7
March	85.8	77.9	66.8	March	164.4	68.1	111.9
April	88.5	71.2	63.0	April	173.4	64.0	110.9
May	86.3	77.4	66.8	May	169.3	74.7	126.5
June	83.6	75.1	62.8	June	155.0	75.9	117.7
July	81.4	74.6	60.7	July	146.3	72.5	106.0
August	87.3	54.2	47.3	August	145.2	62.3	90.4
September	99.4	57.6	57.3	September	143.6	68.2	98.0
October	100.3	58.9	59.1	October	128.1	72.6	93.0
November	101.5	69.5	70.5	November	112.9	74.3	83.9
December	96.9	56.4	54.7	December	99.4	60.0	59.6
1917				1921			
Average	133.8	60.9	81.5	Average	82.3	73.6	60.6
January	107.3	50.0	53.7	January	95.9	72.8	69.8
February	120.8	47.4	57.2	February	92.2	68.5	63.2
March	126.7	55.0	69.7	March	91.8	69.0	63.3
April	140.0	56.9	79.7	April	87.5	65.1	57.0
May	137.4	60.3	82.8	May	78.0	80.8	63.0
June	131.0	56.2	73.6	June	73.4	92.1	67.6
July	124.0	48.1	59.6	July	80.0	74.0	59.2
August	135.1	59.5	80.4	August	85.8	82.8	71.0
September	144.0	67.4	97.1	September	83.9	73.5	61.7
October	144.9	74.3	107.6	October	78.6	79.8	62.7
November	139.0	81.1	112.7	November	72.4	68.6	49.7
December	141.2	62.6	88.4	December	70.5	61.6	43.4

Table 1—Continued

	Price	Quantity	Gross cash income		Price	Quantity	Gross cash income
1922				1925			
Average	81.6	83.1	67.8	Average	104.3	100.2	104.5
January	75.0	74.1	55.6	January	101.6	110.1	111.9
February	86.8	74.5	64.7	February	99.5	97.0	96.5
March	85.3	77.4	66.1	March	105.0	96.4	101.2
April	88.1	70.6	62.2	April	105.9	98.4	104.2
May	90.1	94.3	85.1	May	106.1	98.7	104.7
June	87.9	96.4	84.7	June	108.1	101.0	109.2
July	84.4	87.4	73.8	July	107.3	94.9	101.8
August	75.4	87.1	65.7	August	104.5	113.3	118.4
September	74.3	81.2	60.4	September	102.7	104.8	107.6
October	75.2	80.9	60.9	October	103.6	89.2	92.4
November	79.4	85.1	67.6	November	105.1	95.8	100.7
December	82.5	88.8	73.3	December	104.0	103.2	107.3
1923				1926			
Average	83.6	90.7	75.8	Average	107.6	97.7	105.1
January	87.8	103.9	91.2	January	112.6	97.9	110.2
February	87.5	82.7	72.4	February	115.2	97.1	111.9
March	85.1	90.0	76.6	March	111.4	106.2	118.3
April	90.0	86.2	77.6	April	112.4	103.9	116.8
May	89.0	92.4	82.2	May	110.1	105.9	116.6
June	82.2	90.9	74.7	June	109.5	103.5	113.3
July	79.7	85.8	68.4	July	107.4	104.4	112.1
August	81.0	94.1	76.3	August	100.5	91.8	92.3
September	85.4	91.9	78.5	September	102.8	85.1	87.5
October	79.7	87.6	69.8	October	103.5	93.2	96.5
November	79.6	94.0	74.9	November	104.4	95.9	100.1
December	78.3	87.5	68.5	December	104.3	93.3	97.3
1924				1927			
Average	88.7	101.9	90.4	Average	103.0	93.9	96.7
January	85.5	90.9	77.7	January	112.4	94.0	105.7
February	88.2	103.7	91.5	February	113.4	90.9	103.1
March	84.0	95.8	80.5	March	108.9	93.9	102.3
April	82.4	96.1	79.2	April	110.4	94.4	104.2
May	84.3	94.1	79.3	May	109.0	104.4	113.8
June	84.2	93.0	78.3	June	99.8	103.3	103.1
July	84.8	100.6	85.3	July	97.8	94.0	91.9
August	95.2	93.9	89.4	August	99.9	87.7	87.6
September	93.6	111.9	104.8	September	99.5	94.3	93.8
October	93.0	119.8	111.4	October	98.1	94.5	92.7
November	91.9	107.8	99.0	November	96.3	94.5	91.0
December	92.3	103.6	95.6	December	95.0	84.3	80.1

This price index series shows that Minnesota farm prices were lowest during 1911. There was a gradual increase up to 1915. The years 1916, 1917, and 1918 were marked by sharp increases in prices. Prices during 1919 averaged the highest for any year in the series. They continued to increase during the early months of 1920, reached the peak in April, and fell sharply during the remainder of the year. The decline continued throughout 1921, the low point being reached in December, when the index was 70.5. Prices continued low during 1922, and altho there was some recovery from the December 1921 figure, the average of 1922 was slightly below that of 1921. The year 1923 witnessed a slight recovery, which became more evident during 1924 and continued through 1925 and a part of 1926. The index during the latter part of 1926 was below that of the corresponding months of 1925. Prices for the first half of 1927 were above the base period normal, but from June to October they declined to a point close to normal and in November and December dropped below.

The price index will be continued and made available monthly in the current publications of the Division of Agricultural Economics.

PRICE INDEXES FOR THREE MAJOR GROUPS OF PRODUCTS

A price index of the sixteen principal agricultural products of Minnesota embraces a field of considerable diversification. The index for all these products taken together may obscure the fluctuations in price movements which existed in the separate groups of products. Price indexes have, therefore, been made for the three major groups of Minnesota products, namely, livestock, dairy and poultry products, and crops. The livestock group includes prices of hogs, cattle, calves, lambs-sheep; the dairy and poultry group includes butterfat, milk, eggs, and chickens; the crops group includes the remainder of the sixteen products—wheat, corn, oats, barley, rye, flax, hay, and potatoes. The method of constructing the price indexes of these separate groups was the same as that used for the composite index of all products. An average of the corresponding months of 1924-25-26 has been used as the base for the monthly indexes, and the averages of the period 1924-25-26 for the annual indexes. The monthly and yearly indexes of these three groups are given in Table 2.

The monthly indexes are shown in Figure 3. The index of the crops group appears noticeably above the other groups in 1911-12, 1915, and again in the latter part of 1916, when it started the rapid rise to an index of 190.5 in May, 1917. Following this, for a period of almost two years, the index had a downward trend, doubtless owing to some extent to governmental control of prices. In March, 1919, the index started on a renewed upward climb which continued until the extremely high point of 242.9 was reached in April, 1920. The price index for the livestock group was somewhat above the other groups in 1913 and 1914. Near the close of 1916 this index followed the rise of the crops group, but rose less sharply and experienced less setback in 1918 than the crops group. The high point of the livestock index was reached in July, 1919, when the index stood at 185.6. Comparisons of price movements of the livestock group with the other groups are affected to some extent by the existence of hog and beef cattle cycles. The dairy and poultry index also began to rise in 1916, rose more slowly than either of the others, and continued, with a very gradual upward trend, to its high point of 165.3 in May, 1920.

The behavior of these group indexes during the period of rising prices is in striking contrast with their behavior during the period of falling prices, 1919-20-21. The livestock price index which reached the second highest peak was the first to take a decided drop and by the latter part of 1921, approximately 27 months after the fall began, had reached a point slightly lower than either of the other groups. The crops index fell after April, 1920 and by December, 1921 it had fallen almost as low as the low point of the livestock index. The period of fall was shorter in the crops index than in livestock by seven or eight months so that this group which had experienced the most spectacular rise, in turn experienced the sharpest decline. The dairy and poultry index, which was last to rise and rose least, was the last to fall (by a margin of one month) and as a whole fell considerably less than the other two groups. Moreover, the fall in this index was completed in a period of approximately one year. For the latter part of 1922, and for 1923 and the first half of 1924, the dairy and poultry index maintained a position conspicuously above the indexes of the other two groups.

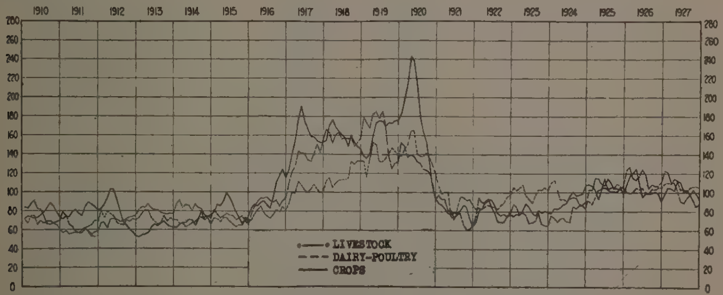

Fig. 3. Price Indexes of Livestock, Dairy and Poultry Products, and Crops by Months, 1910-1927
(Average of corresponding months of 1924-25-26=100)

QUANTITY INDEX FOR ALL COMMODITIES MARKETED

Altho the agricultural price index is a subject of considerable interest, from a practical standpoint a question often arises as to the volume of products marketed concurrently with a changing price level. When prices are high, is the assumption justified that quantities as a whole are necessarily small, and when prices are low, the quantities large, as is frequently the case with a single commodity? To answer such questions, the price index of agricultural products needs to be supplemented by a quantity index of the agricultural products marketed. Such an index has been computed for Minnesota farm products by methods

Table 2.

Monthly and Yearly Price Indexes of Livestock Products, Dairy and Poultry Products, and Crops, for Minnesota, 1910-1927

(Average of corresponding months of 1924-25-26=100.)

	Livestock	Dairy poultry	Crops
1910			
Average	76.9	68.6	79.1
January	84.0	70.1	71.4
February	83.2	67.6	74.4
March	87.8	74.9	73.9
April	91.3	75.3	72.1
May	82.3	65.8	73.3
June	81.7	69.8	75.6
July	75.2	67.8	78.8
August	66.0	68.6	83.3
September	65.8	69.8	88.2
October	66.4	66.4	85.2
November	68.2	65.8	79.9
December	69.8	60.3	73.2
1911			
Average	62.2	60.5	81.0
January	78.8	57.0	71.2
February	74.4	58.6	74.4
March	65.5	55.5	73.9
April	63.1	56.7	78.8
May	58.1	57.0	81.1
June	56.2	56.9	77.3
July	57.3	60.0	74.8
August	60.3	62.0	84.5
September	58.2	63.3	89.2
October	55.6	65.5	87.2
November	57.5	69.3	84.2
December	58.5	69.1	80.8
1912			
Average	70.2	71.8	71.6
January	66.9	80.8	81.9
February	67.3	72.2	86.9
March	61.8	79.7	93.5
April	71.1	77.0	103.1
May	71.5	74.4	103.3
June	70.7	67.2	93.1
July	68.9	65.9	79.4
August	69.2	65.3	69.1
September	71.3	70.7	65.1
October	73.0	68.6	60.3
November	74.0	71.5	57.7
December	75.0	70.3	53.7
1913			
Average	80.6	72.6	62.3
January	81.2	72.7	52.5
February	84.0	77.6	55.2
March	83.6	80.9	55.1
April	87.6	80.4	57.0
May	82.5	72.2	62.4
June	81.1	69.2	66.0
July	81.2	66.0	64.0
August	78.5	67.5	66.3
September	77.2	75.1	68.7
October	76.6	69.0	65.3
November	77.4	72.2	63.2
December	76.9	70.2	62.2
1914			
Average	81.8	68.3	71.4
January	87.5	70.5	62.0
February	91.5	66.4	65.6
March	83.2	66.7	67.2
April	86.3	63.0	67.8
May	85.8	64.8	70.6
June	80.4	67.3	70.3
July	87.1	68.6	64.6
August	83.2	72.5	71.8
September	82.0	73.6	80.3
October	75.5	71.0	73.1
November	74.3	72.7	74.1
December	72.2	66.4	76.0
1915			
Average	73.7	69.0	78.1
January	80.4	72.4	79.6
February	76.7	71.9	87.1
March	72.3	68.5	86.5
April	74.7	73.5	90.9
May	77.7	72.5	99.3
June	75.8	68.6	94.2
July	75.1	66.0	87.3
August	70.8	63.5	79.8
September	72.2	64.7	73.2
October	74.7	65.2	67.0
November	69.6	73.9	71.1
December	66.5	67.9	75.1
1916			
Average	89.2	78.3	99.4
January	77.8	71.0	83.3
February	85.3	76.8	87.1
March	90.4	81.6	85.3
April	91.9	84.9	88.9
May	91.9	78.5	90.4
June	92.2	75.1	86.2
July	90.9	72.2	82.9
August	89.9	76.0	94.6
September	91.7	81.3	110.9
October	85.6	79.5	117.8
November	90.5	84.5	122.4
December	94.2	80.4	115.0
1917			
Average	136.6	101.9	155.7
January	108.8	87.9	121.7
February	121.4	100.0	140.0
March	126.6	98.4	155.2
April	143.1	111.4	177.2
May	141.5	107.7	190.5
June	141.2	102.1	175.1
July	134.2	99.5	166.5
August	132.6	102.5	158.5
September	139.7	108.1	158.3
October	150.4	103.8	154.4
November	142.1	99.3	152.3
December	155.3	100.0	152.2

Table 2—Continued

	Live-stock	Dairy poultry	Crops		Live-stock	Dairy poultry	Crops
1918				1922			
Average	157.0	117.9	156.7	Average	83.5	86.6	81.3
January	166.0	112.0	154.8	January	75.5	82.4	68.9
February	162.6	115.4	170.2	February	94.4	83.9	80.8
March	151.6	105.1	176.3	March	90.0	82.5	83.2
April	160.1	109.9	168.1	April	89.4	85.2	90.6
May	163.5	112.3	164.5	May	92.2	86.5	93.6
June	156.1	113.6	160.4	June	92.6	85.0	84.9
July	157.5	113.5	157.5	July	86.8	85.4	78.5
August	156.6	115.2	149.1	August	78.4	82.1	69.1
September	157.6	132.4	160.4	September	76.0	86.6	68.7
October	149.2	129.8	153.0	October	77.2	89.2	69.1
November	152.4	133.1	148.3	November	75.4	95.6	74.8
December	157.9	133.3	146.0	December	78.1	97.9	77.5
1919				1923			
Average	160.5	138.5	164.7	Average	73.7	100.4	79.1
January	179.5	133.2	138.3	January	87.9	105.6	74.8
February	173.4	115.6	136.3	February	85.3	102.1	77.4
March	167.9	137.8	141.7	March	76.8	105.0	76.2
April	182.4	153.3	160.6	April	78.9	108.3	81.3
May	184.7	150.5	173.4	May	76.4	97.2	88.5
June	178.5	133.0	175.5	June	67.7	93.6	84.6
July	185.6	132.7	175.2	July	68.5	89.9	78.9
August	170.3	135.8	169.6	August	70.1	97.2	75.8
September	138.4	141.1	173.7	September	78.3	103.1	81.3
October	125.2	147.1	172.9	October	67.2	102.8	79.2
November	130.4	143.6	175.8	November	65.7	105.6	80.3
December	132.2	138.7	175.7	December	64.4	101.2	79.4
1920				1924			
Average	128.7	142.8	163.0	Average	77.3	95.9	94.2
January	152.8	138.4	183.9	January	75.8	110.1	78.2
February	149.1	145.5	196.1	February	73.4	113.2	83.5
March	137.2	150.2	215.2	March	69.5	103.2	82.6
April	139.4	164.5	242.9	April	72.5	92.5	84.2
May	138.3	165.3	238.5	May	73.6	93.1	87.9
June	133.2	141.0	212.7	June	69.3	91.0	89.3
July	130.6	138.0	178.5	July	68.9	93.9	96.7
August	124.6	138.1	163.9	August	85.3	94.9	100.9
September	123.8	141.5	153.6	September	83.6	94.3	96.6
October	120.7	136.1	129.8	October	86.3	86.8	97.8
November	109.4	129.6	107.7	November	86.4	87.9	98.9
December	92.1	119.3	92.8	December	83.0	89.9	107.9
1921				1925			
Average	77.0	90.0	80.8	Average	107.8	101.7	103.0
January	97.1	106.6	88.1	January	102.3	91.0	108.4
February	93.0	98.2	86.5	February	102.3	87.5	107.2
March	93.1	100.1	82.9	March	115.5	95.2	102.2
April	81.2	100.2	77.9	April	115.6	102.5	92.7
May	81.3	75.4	77.3	May	109.6	103.8	104.1
June	71.4	71.7	78.6	June	107.5	105.4	115.0
July	76.8	83.7	78.1	July	114.9	103.5	103.2
August	78.7	95.3	80.7	August	110.9	105.3	101.4
September	66.4	94.7	86.4	September	104.4	104.8	101.3
October	60.5	91.8	84.4	October	104.3	109.4	100.9
November	61.3	92.5	72.8	November	103.8	106.4	105.7
December	64.5	86.7	64.2	December	107.1	104.6	99.2

Table 2—Continued

	Livestock	Dairy poultry	Crops		Livestock	Dairy poultry	Crops
1926				1927			
Average	114.6	102.6	104.4	Average	103.3	107.4	98.0
January	123.5	100.5	108.8	January	123.0	109.3	98.3
February	126.7	99.1	117.9	February	121.9	110.3	105.4
March	114.7	100.4	121.1	March	111.4	109.7	104.1
April	113.7	104.8	124.7	April	110.1	114.4	102.0
May	116.7	103.7	110.9	May	102.4	113.5	113.0
June	122.4	104.8	95.6	June	90.6	103.2	111.3
July	118.4	100.6	99.2	July	89.7	103.6	101.4
August	104.2	99.2	99.4	August	94.2	101.1	102.8
September	108.2	103.9	99.7	September	97.8	104.9	98.0
October	107.0	103.6	101.4	October	103.4	106.3	91.2
November	107.9	105.4	99.2	November	98.4	106.2	85.5
December	110.3	105.3	91.6	December	92.6	105.0	88.0

similar to those used in computing the price index.[11] The result is an index which shows changes in the quantities of products sold by Minnesota farmers, measured from a base period of 1924-25-26 for the yearly indexes, and from an average of the marketings of each corresponding month of 1924-25-26 for the monthly indexes. A quantity index of 94.5 for October, 1927, shows that the quantity marketed in this month was 5.5 per cent less than the average of the three Octobers in 1924-25-26. The seasonal fluctuations in marketing which prevailed in the period 1924-25-26 are thus eliminated from the quantity index in the same manner and subject to the same limitations as in the price index.

The quantity index is not an index of changes in agricultural production but of the amounts of agricultural products sold by farmers. The data of amounts sold are difficult to obtain by months for all products, and the methods employed in arriving at the approximate figures are explained in full in a later section of this bulletin. These quantities, however, are necessary as weights in the formula selected for the price index (and the index of gross income) so that no additional data need be gathered for the computation of the quantity index.

The quantity index as computed to show changes in the marketings of Minnesota farm products by months and years is shown in the second column of Table 1. The monthly quantity indexes are shown graphically in Figure 4.

[11]

$$\sqrt{\frac{\Sigma[q_1 \quad p_{0(cm)}]}{\Sigma[q_{0(cm)} \quad p_{0(cm)}]} \times \frac{\Sigma[q_1 \quad p_1]}{\Sigma[q_{0(cm)} \quad p_1]}}$$

q_1 = quantity marketed in current month.
p_1 = price in current month.
$q_{0(cm)}$ = average quantity marketed in corresponding months of 1924-25-26.
$p_{0(cm)}$ = average price in corresponding months of 1924-25-26.

This index of quantity of products sold discloses a surprising trend in production. The quantities sold during 1911 were the lowest for any year of the period. Thereafter there was a rather steady rise in marketings with slight recessions in 1914, 1916, and the early part of 1917. The quantity of marketings increased sharply in 1918, declined in 1919 and 1920, and then increased steadily to a high point of 119.8 in October, 1924. From that time to the end of 1927 there has been a gradual decline in the quantity index. For the period as a whole there has been a decided upward trend in physical volume of production as indicated by farm marketings.

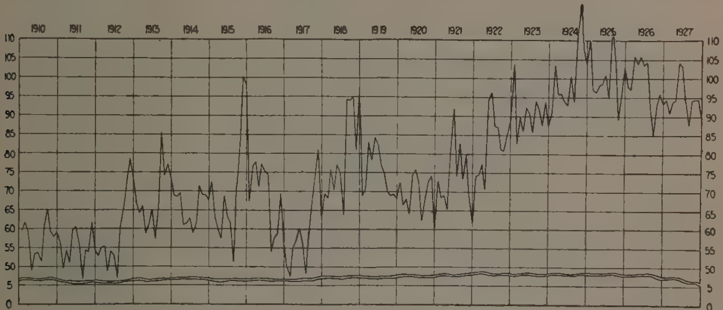

Fig. 4. Quantity Indexes of Minnesota Farm Products Marketed by Months, 1910-1927 (Average of corresponding months of 1924-25-26=100)

The increase that represents Minnesota conditions is probably not representative of the entire country. Much of the increase has been due to the increase of livestock, livestock products, and corn. Absolute decreases or only slight increases in production have existed in several of the products which made up the bulk of farm production during the early part of the period under consideration. Probably not many states have experienced the rapid changes which have taken place in Minnesota in the types of commodities produced. Hence the Minnesota quantity index reflects conditions which may not be duplicated in many other sections of the country.

INDEX OF GROSS CASH INCOME

The index of gross cash income of the Minnesota farmers is only a short step beyond the computation of price and quantity indexes. When a type of formula has been selected for the calculation of these two indexes which conforms to the factor reversal test, the index of gross cash income is the product of the price index by the quantity index for the same period. The index of gross cash income by months and years is shown in the third column of Table 1, and is equivalent to a product of the figures in the first and second columns. The monthly indexes of gross cash income are shown in Figure 5.

Gross cash incomes for Minnesota were lowest in 1911. A steady rise followed until 1916 and a sharp rise during 1917 and 1918. The peak was reached in September, 1918 when the index of gross cash income was 145.5. In May, 1919 the index rose again to a point almost as high, 142.4. The decline in income during the latter part of 1919 appears to have been influenced by the lower average quantity of farm marketings during that period. There was a continued reduction of income in 1920 and a further decline in 1921, when the average gross cash income reached the level of 1916. There was an improvement in 1922 to 1924, when a low price index prevailed with an increasing quantity index. A general rise continued until 1926, but during 1927 the index of gross income was consistently lower than in 1926.

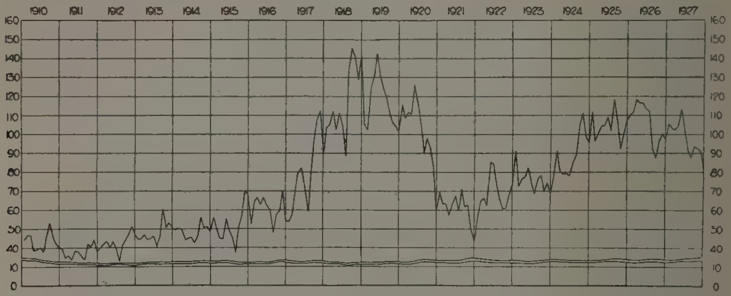

Fig. 5. Indexes of Gross Cash Income of Minnesota Farmers by Months, 1910-1927 (Average of corresponding months of 1924-25-26=100)

Heretofore the importance of quantity sales as a determinant of farm incomes probably has been underemphasized. The foregoing indexes of prices and quantities show that, at least for Minnesota, the quantity of production has been exerting a marked effect upon farm incomes.

GROSS CASH INCOME IN DOLLARS

The gross cash income of the farmers of Minnesota has thus far been expressed only in terms of index numbers which unquestionably furnish the most satisfactory method of representing the general trend of income. The actual work of making this series of index numbers, however, involved specific prices and definite quantities, and as a result the gross farm income from the sales of the sixteen commodities included in the index was computed in actual dollars. Fewer commodities than sixteen could have been used for the index and approximately the same trend of price level would have resulted, but as nearly all of the major products were included, the actual amounts in dollars are of interest as a gross cash income figure for the state, provided their limitations are kept in mind. A further discussion of these limitations will be given, but in general they are two: First, only the sixteen major products are included and, second, insufficient data have necessitated that a number of the quantities be estimated by a variety of methods.

In calculating the *total* income of an industry necessarily many items must be estimated. In calculating *cash* income the number of estimated items is reduced. This is particularly true of the cash income from agriculture. Total income is made up of the cash sales of products together with the estimated value of the products used directly by the farm. This latter group constitutes a significant proportion of the total income and because the basis for the valuation of these items is uncertain and in most cases the quantities of the products used are not known, the calculated total income would probably involve a larger error than would a cash income grounded on more satisfactory basic information.

Altho calculation of cash income involves fewer estimates than total income, a considerable number still remain to be made. Probably no data purporting to show the exact marketings and value of cash income by sources represent complete enumerations. They are estimates, but, as there are ordinarily several ways in which such estimates can be checked for gross errors, they closely approximate the actual condition. Estimates of production and sales can, for example, be compared with railroad shipments, with receipts at markets, with raw materials purchased by manufacturers, or with the output of industries. Material errors in the original estimate will thus be revealed through the inconsistencies arising from comparison with these or other indexes of sales.

The principal sources of data from which the cash income of farmers must be calculated are the publications of the United States Bureau of the Census and the United States Department of Agriculture. Many years of experience in making estimates and developing the technic of estimation make the data from these sources reasonably reliable. The census data are derived from actual enumeration but practically all of the final figures are estimates based upon enumeration, and comparatively few figures represent the mere summation of the original data. Inconsistencies in the raw data are adjusted so that only figures in which obvious discrepancies have been eliminated, are finally published. The census data probably err by being too low. The failure of enumerators to interview every producer or to ask all questions, together with the reticence of the people being interviewed, tend to give a downward bias to the raw census data.

The United States Department of Agriculture has developed an elaborate system of obtaining information. Its crop estimators become continually more efficient and when their reports are consolidated and analyzed by the expert estimators in the central department the final results without doubt are as accurate as if based on enumeration. Its prices of products, time of marketing, and similar data are not available elsewhere and furnish the only source of many items essential to the calculation of farm income.

By supplementing these two principal sources with data secured from reports of bureaus of markets, state food commissions, trade publications, reports of manufacturers, receipts at markets, and railway statistics, sufficient material may be collected to prepare reliable estimates of cash incomes. The data of minor products such as wool, truck crops, fruits, honey and wax, and of more important commodities, such as dairy products, poultry and eggs, and hay, are particularly unsatisfactory. Inaccuracies in the figures, or even entire omission of the first group for which the data are especially poor, introduce little error, because the total value of those commodities is small in comparison with other sources of cash income. The latter group is important and without doubt the most painstaking estimate of farm income will be somewhat inaccurate because of the poor basic data. For whole milk, poultry, and eggs there are no well established central markets through which the bulk of the production flows as in the case of other farm products. Milk is generally sold locally. There is no way of obtaining accurate data of the amount produced and sold. An estimate can be made, but the assumptions necessary to such an estimate may be so arbitrary that the estimate itself is open to serious question. The census estimates of milk sold are probably quite unsatisfactory. Few farmers can give the enumerator little more than a guess as to the amount of whole milk sold in a year. The time of taking the census probably causes these estimates of the farmers to have a downward bias. In the winter or early spring, milk production is low and the producer is inclined to base his estimate of the annual production upon the current production. A similar situation exists with respect to poultry and eggs. Farmers do not keep accurate records of sales of these products. They are sold in small amounts and often are consumed locally. There is no way in which sales of such products can be checked properly against receipts in central markets. The data on hay—production, sales, and prices—are also unsatisfactory. Altho records of shipments to market are ordinarily available, the amount sold locally between farms is unobtainable. Hay is a product that is poorly classified by grade, hence it is difficult to apply price data in such a way as to represent properly the total value of the crop sold.

These observations apply particularly to the problem of the calculation of an estimate of the income of the whole agricultural industry. Where the problem is restricted to the estimation of the income for a state, all of the above difficulties are effective, and, in addition, many others which are brought into existence by the attempt to divide the data of the industry by state lines.

The census and department of agriculture estimates are prepared by states, but such estimates are not as easily checked for accuracy by reference to supplementary data as are the totals for the country. The receipts at markets are not readily classified by points of origin. Manufacturers do not report the sources of their raw material. Railroad shipments by states are not generally available. The data of raw material and products used by factories or received at markets within the state are of some assistance, but adjustment must be made for the quantity obtained from farmers outside the state boundaries. Likewise correction must be made for the amounts of products sold by farmers in markets outside of the state. Often these necessary adjustments must be made without adequate evidence upon which to base them. Because of these additional sources of error it is probable that the division of total income by states is less accurate than the estimate of income from agriculture as a whole.

In general, however, price, production, and sales data are reasonably satisfactory. Particularly is this true of the various grain and livestock crops, where such errors as may exist in the data of one crop are compensated largely by errors in another crop. The errors in the gross sales of the agricultural industry are not serious, considering even those possibilities for error which have been noted.

The quantities and prices of the sixteen major products, which are given in a later section of the bulletin, furnish the basis for the estimated gross cash income of the farmers of Minnesota, as shown in Table 3. The quantity of each commodity sold in a month has been multiplied by the price in that month, and the sum of the sales of the sixteen products has been taken as the approximate gross cash income for the month.

Table 3

Monthly Gross Cash Income of Farmers of Minnesota,* 1910-1927

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	$ 14,797,464	$ 13,144,012	$ 13,237,200	$ 14,675,441	$ 16,457,196	$ 18,715,009	$ 17,437,884	$ 17,769,996	$ 34,287,644
February	13,733,473	10,204,825	12,380,333	13,203,945	14,857,424	14,696,035	18,931,872	16,856,968	30,805,399
March	14,985,547	11,491,287	13,899,295	15,085,746	16,037,416	14,473,003	21,439,636	22,354,131	35,956,621
April	10,542,171	9,139,285	10,878,821	12,045,791	11,987,570	12,221,915	17,140,285	21,671,103	27,841,697
May	10,158,050	9,920,803	11,269,512	11,630,575	11,765,921	14,457,299	17,350,213	21,506,314	28,905,549
June	11,228,032	10,618,875	10,967,847	12,992,678	12,640,623	13,587,064	17,491,205	20,509,496	29,210,321
July	9,958,693	9,429,099	8,656,717	10,643,496	11,279,146	12,020,915	16,024,652	15,716,326	23,417,286
August	14,126,808	10,281,366	12,590,168	13,822,486	13,946,366	11,298,136	14,425,407	24,506,391	40,634,220
September	18,728,045	14,828,833	15,484,876	21,407,954	19,877,768	17,828,159	20,118,827	34,119,239	51,119,835
October	18,144,376	15,975,428	18,470,446	20,099,463	20,057,266	22,594,290	23,317,644	42,466,899	55,776,189
November	13,905,733	14,596,426	16,806,871	17,493,982	16,720,516	23,132,303	23,117,015	36,955,577	38,957,139
December	15,552,215	14,482,721	17,988,600	19,297,522	18,760,028	26,343,265	20,928,317	33,832,035	53,956,916
Total	$165,860,607	$144,112,960	$162,630,686	$182,399,079	$184,387,240	$201,367,393	$227,722,957	$308,264,475	$450,868,816

	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	$ 35,029,418	$ 38,483,231	$ 23,089,476	$ 18,518,347	$ 30,192,778	$ 25,730,714	$ 37,033,404	$ 36,458,656	$ 34,968,230
February	30,130,833	32,025,891	18,628,116	19,048,742	21,321,081	26,938,658	28,421,067	32,956,150	30,362,126
March	39,998,802	35,922,618	20,301,442	21,219,736	24,564,010	25,819,472	32,469,198	37,951,428	32,812,071
April	35,468,609	30,165,357	15,514,249	16,940,599	21,119,648	21,544,165	28,354,815	31,785,675	28,348,410
May	37,014,844	32,864,921	16,376,183	22,096,642	21,362,624	20,606,473	27,203,755	30,311,620	29,574,587
June	36,580,812	32,793,790	18,828,371	23,599,057	20,799,705	21,817,726	30,439,142	31,580,246	28,724,250
July	32,960,069	27,967,536	15,628,313	19,487,075	18,059,473	22,504,758	26,852,446	29,593,896	24,249,956
August	36,556,881	27,544,232	21,640,869	20,028,312	23,248,034	27,233,100	36,096,523	28,136,223	26,704,741
September	39,064,616	34,441,957	21,694,181	21,231,611	27,586,724	36,839,443	37,799,346	30,742,185	32,973,174
October	41,851,992	36,715,099	24,729,836	24,042,766	27,545,523	43,973,355	36,461,049	38,066,696	36,576,704
November	34,134,588	27,490,260	16,291,503	22,154,927	24,567,227	32,460,820	33,023,993	32,822,925	29,838,818
December	38,761,122	22,815,617	16,585,845	28,034,632	26,222,650	36,557,377	41,062,958	37,206,200	30,644,243
Total	$437,552,586	$379,230,509	$229,308,384	$256,402,446	$286,589,477	$342,026,061	$395,217,696	$397,611,900	$365,777,310

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* Cash income from sales of the following products: wheat, corn, oats, barley, rye, flax, hay, potatoes, hogs, cattle, calves, lambs-sheep, chickens, eggs, butterfat, and milk.

Table 4

Annual Gross Cash Income from the Sales of Principal Products by the Farmers of Minnesota, 1910-1927

	1910	1911	1912	1913	1914	1915	1916	1917	1918
Wheat	$ 57,847,277	$ 43,555,757	$ 43,093,415	$ 46,720,610	$ 44,059,073	$ 53,967,169	$ 46,587,912	$ 78,288,759	$132,476,411
Corn	8,007,245	6,451,533	5,423,597	9,670,870	13,496,855	7,478,267	4,202,198	10,853,329	21,869,461
Oats	9,292,624	4,646,278	7,980,297	12,218,785	9,949,074	12,589,708	13,395,735	11,467,479	26,637,875
Barley	7,848,530	10,919,406	9,652,349	7,883,977	8,044,683	9,265,094	11,235,525	16,191,227	14,843.963
Rye	2,400,520	3,451,473	2,967,951	2,711,759	3,681,305	4,893,655	5,475,360	8,060,988	10,765,755
Flax	6,729,516	4,984,930	4,892,753	4,718,627	3,910,244	4,107,154	4,951,390	4,409,505	8,561,923
Hay	1,926,021	1,706,538	2,125,359	1.786,236	2,146,670	2,682,525	2,859,118	3,497,622	4,341.893
Potatoes	5,242,000	7,601,250	8,469,840	6,834,670	7,673,320	5,768,940	10,532,360	14,389,670	12,880,010
Hogs	20,103,041	17,213,080	21,025,147	28,782,931	29,103,560	28,215,687	44,208,343	53,695,616	81,857,709
Cattle	9,817,987	11,098,886	13,383,134	15,241,038	18,586,414	27,211,556	30,317,185	39,450,344	52.027,233
Calves	1,279,726	1,007,564	1,260,834	1,510,437	1,813,196	2,013,005	2,565,068	3,789,337	4,952,962
Lambs-Sheep	863,193	782,996	981,966	803,098	1,045,979	858,031	915,937	1.198,339	1,948,503
Chickens	2,062,242	1,965,644	2,812,854	2,370,174	2,388,978	2,357,543	3,038,540	3,734,041	4,800,000
Eggs	5,399,933	4,623,404	5,657,089	5,735,251	6,055,104	6,102,191	7,317.956	11,306,036	12,671,693
Butterfat	22,829,491	20,331,723	28,299,279	30,554,947	27,607,331	28,890,305	34,305,107	39,857,921	50,446,206
Milk	4,211,261	3,772,498	4,604,822	4,855,669	4,825,454	4,966,563	5,815,223	8,074,262	9,787,159
Total	$165,860,607	$144,112,960	$162,630,686	$182,399,079	$184,387,240	$201,367,393	$227,722,957	$308,264,475	$450,868,816

	1919	1920	1921	1922	1923	1924	1925	1926	1927
Wheat	$ 90,133,153	$ 54,962,938	$ 26,931,043	$ 23,746,514	$ 21,448,023	$ 34,918,877	$ 42,060,061	$ 35,430,564	$ 21,617,831
Corn	19,445,481	23,334,825	14,143,687	15,078,331	17,283,139	23,314,958	17,481.396	12,987,292	7,475,441
Oats	15,902,438	18,384,619	8,328,958	9,493,783	13,370,711	25,454,718	22.491,710	11,104,204	7,964,469
Barley	18,814.493	12,696,554	3,284,160	3,622,786	4,321,467	7,236,122	8,802,227	5,373,925	6,911,305
Rye	10,619,884	12,164,516	8,496,485	10,185,228	9,846,830	12,736,304	6,488.352	3,405,634	5,270,189
Flax	11,979,396	8,613,637	4,692,997	5,580,937	11,650,074	14,246,329	18,925,064	15,069,724	13,604.432
Hay	6,075,140	7,482,065	4,869,155	4,744,935	5,043,124	5,190,308	5,652,437	4,973,986	5,539,657
Potatoes	21,375,710	23,382,770	16,920,160	11,916,470	10,538,380	10,229,410	14,567.460	22,783,250	18,564,579
Hogs	93,908,373	73,555,446	45,416,265	63,691,054	63,377,109	69,819,251	100,447,084	113,497,681	18,564,579
Cattle	44,200,782	38,841,294	20,454,793	25,158,705	23,647,832	25,618.131	32,175,165	40,413,097	94,984,139
Calves	4,873,952	5,118,025	2,995,369	4,266,826	4,561,291	4,782,595	6,666,531	8,035,386	40,754,756
Lambs-Sheep	2,826,797	2,471,456	1,543,685	2,020,429	1,698,043	2,128,434	2,708,796	3,817,776	8,240,875
Chickens	5,085,347	5,942,294	4,836,725	4,441,715	3,900,266	5,161,893	5,378,411	7,066,165	4,017,739
Eggs	14,309,183	15,971,276	10,212,922	9,877,759	10,767,048	10,823,695	13,655,787	13,919,674	6,375,239
Butterfat	65,318,812	64,715,344	47,432,369	54,295,530	73,926,212	79,709,404	85.481,420	87,184,276	12,086,867
Milk	12,683,645	11,593,450	8,749,611	8,281,444	11,209,928	10,655,632	12,235,795	12,549,266	99,489,164
Total	$437,552,586	$379,230,509	$229,308,384	$256,402,446	$286,589,477	$342,026,061	$395,217,696	$397,611,900	$365,777,310

A diagram showing the comparison of total annual cash incomes is presented in Figure 6, where the annual amounts are represented by the height of the bars. After 1911 the gross income increased gradually until 1917. In 1917 and 1918 the increase was marked. A slight decline came in 1919, a further decline in 1920, and in 1921 it struck the lowest figure in the post-war period. In 1922 it began to rise again and the rise continued through 1926, altho the increase of 1926 over 1925 was slight. The total income for 1927 was noticeably less than that for 1926. Computations which have been made for 1928 indicate that the gross cash income will show an increase of only about a million dollars over the total for 1927.

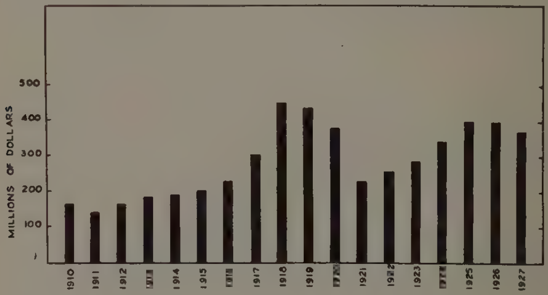


Fig. 6. Gross Cash Income of Minnesota Farmers, 1910-1927

The amounts which each of the sixteen products contributed to the annual gross receipts are shown in Table 4, and a comparison of the relative importance of the various products in the gross income for each year can be had by an examination of Table 5 which shows the percentage which the cash receipts from each crop formed of the gross cash income for the calendar year.

The facts of Table 5 are more clearly brought out in the series of bar diagrams for the years 1910 to 1927, shown in Figure 7. Wheat constituted the largest single percentage of the yearly receipts for each year from 1910 to 1918, inclusive, after which hogs took first position in the years 1919, 1920, 1922, 1925, and 1926, and butterfat in 1921, 1923, 1924, and 1927. Wheat dropped as low as fourth position in the years 1922, 1923, 1926, and 1927 when its contributions to the cash income were 9.3, 7.5, 8.9, and 5.9 per cent, respectively.

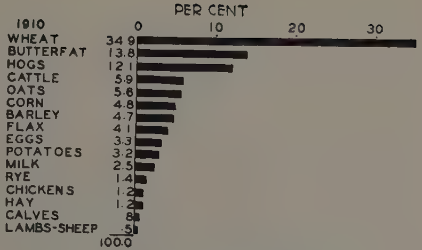
Other interesting facts in the make-up of each year's gross income and changes from year to year may be noted from the graphs. The decided predominance of a single crop in the earlier years, such as approximately 35 per cent of the 1910 income from wheat, has been replaced largely by contributions to the year's income of two or three crops in almost equal measure, as hogs and wheat in 1919 with 21.5 and 20.6 per cent respectively, hogs and butterfat in 1926 with 28.4 and 21.9 per cent respectively, and butterfat and hogs in 1927 with 27.2 and 26.0 per cent respectively.

Table 5

Percentage of Annual Gross Cash Income of the Farmers of Minnesota from the Sales of Principal Crops, 1910-1927

	1910	1911	1912	1913	1914	1915	1916	1917	1918
Wheat	34.9	30.2	26.5	25.6	23.9	26.8	20.5	25.4	29.4
Corn	4.8	4.5	3.3	5.3	7.3	3.7	1.8	3.5	4.8
Oats	5.6	3.2	4.9	6.7	5.4	6.3	5.9	3.7	5.9
Barley	4.7	7.6	5.9	4.3	4.3	4.6	4.9	5.3	3.3
Rye	1.4	2.4	1.8	1.5	2.0	2.4	2.4	2.6	2.4
Flax	4.1	3.5	3.0	2.6	2.1	2.0	2.2	1.5	1.9
Hay	1.2	1.2	1.3	1.0	1.2	1.3	1.3	1.1	1.0
Potatoes	3.2	5.3	5.2	3.7	4.1	2.9	4.6	4.7	2.9
Hogs	12.1	11.9	12.9	15.8	15.8	14.0	19.4	17.4	18.1
Cattle	5.9	7.7	8.3	8.4	10.1	13.5	13.3	12.8	11.5
Calves	0.8	0.7	0.8	0.8	1.0	1.0	1.1	1.2	1.1
Lambs-Sheep	0.5	0.5	0.6	0.4	0.6	0.4	0.4	0.4	0.4
Chickens	1.2	1.4	1.7	1.3	1.3	1.2	1.3	1.2	1.1
Eggs	3.3	3.2	3.5	3.1	3.3	3.1	3.2	3.7	2.8
Butterfat	13.8	14.1	17.4	16.8	15.0	14.3	15.1	12.9	11.2
Milk	2.5	2.6	2.9	2.7	2.6	2.5	2.6	2.6	2.2
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

	1919	1920	1921	1922	1923	1924	1925	1926	1927
Wheat	20.6	14.5	11.7	9.3	7.5	10.2	10.6	8.9	5.9
Corn	4.5	6.2	6.2	5.9	6.0	6.8	4.4	3.3	2.0
Oats	3.6	4.8	3.6	3.7	4.7	7.5	5.7	2.8	2.2
Barley	4.3	3.3	1.4	1.4	1.5	2.1	2.2	1.4	1.9
Rye	2.4	3.2	3.7	4.0	3.4	3.7	1.6	0.9	1.4
Flax	2.7	2.3	2.1	2.2	4.0	4.2	4.8	3.8	3.7
Hay	1.4	2.0	2.1	1.9	1.8	1.5	1.4	1.2	1.5
Potatoes	4.9	6.2	7.4	4.6	3.7	3.0	3.7	5.7	5.1
Hogs	21.5	19.4	19.8	24.8	22.1	20.4	25.4	28.4	26.0
Cattle	10.1	10.2	8.9	9.8	8.2	7.5	8.2	10.2	11.2
Calves	1.1	1.3	1.3	1.7	1.6	1.4	1.7	2.0	2.3
Lambs-Sheep	0.6	0.6	0.7	0.8	0.6	0.6	0.7	1.0	1.1
Chickens	1.2	1.6	2.1	1.7	1.4	1.5	1.4	1.8	1.7
Eggs	3.3	4.2	4.5	3.8	3.8	3.2	3.5	3.5	3.3
Butterfat	14.9	17.1	20.7	21.2	25.8	23.3	21.6	21.9	27.2
Milk	2.9	3.1	3.8	3.2	3.9	3.1	3.1	3.2	3.5
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0


PER CENT
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WHEAT 34.9
BUTTERFAT 13.8
HOGS 12.1
CATTLE 5.9
OATS 5.6
CORN 4.8
BARLEY 4.7
FLAX 4.1
EGGS 3.3
POTATOES 3.2
MILK 2.5
RYE 1.4
CHICKENS 1.2
HAY 1.2
CALVES .8
LAMBS-SHEEP .5
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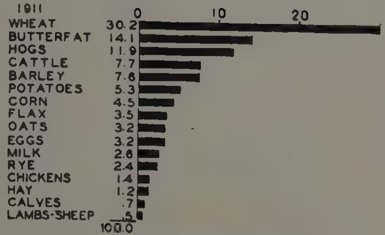
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CATTLE 7.7
BARLEY 7.6
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CORN 4.5
FLAX 3.5
OATS 3.2
EGGS 3.2
MILK 2.6
RYE 2.4
CHICKENS 1.4
HAY 1.2
CALVES .7
LAMBS-SHEEP .5
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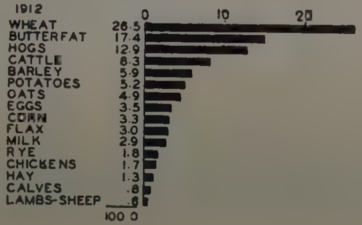
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BUTTERFAT 17.4
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CATTLE 8.3
BARLEY 5.9
POTATOES 5.2
OATS 4.9
EGGS 3.5
CORN 3.3
FLAX 3.0
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CHICKENS 1.7
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CALVES .8
LAMBS-SHEEP .6
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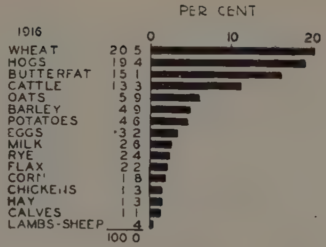
PER CENT
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HOGS 19.4
BUTTERFAT 15.1
CATTLE 13.3
OATS 5.9
BARLEY 4.9
POTATOES 4.6
EGGS 3.2
MILK 2.6
RYE 2.4
FLAX 2.2
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HAY 1.3
CALVES 1.1
LAMBS-SHEEP .4
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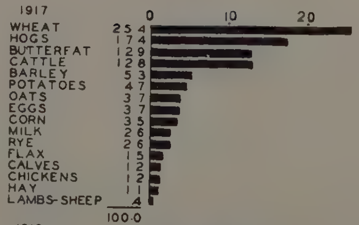
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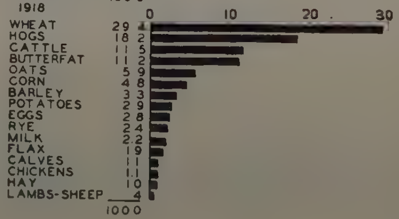
1917
WHEAT 25.4
HOGS 17.4
BUTTERFAT 12.9
CATTLE 12.8
BARLEY 5.3
POTATOES 4.7
OATS 3.7
EGGS 3.7
CORN 3.5
MILK 2.6
RYE 2.6
FLAX 1.5
CALVES 1.2
CHICKENS 1.2
HAY 1.1
LAMBS-SHEEP .4
100.0


0
10
20
30
1918
WHEAT 29.[illegible]
HOGS 18.2
CATTLE 11.5
BUTTERFAT 11.2
OATS 5.9
CORN 4.8
BARLEY 3.3
POTATOES 2.9
EGGS 2.8
RYE 2.4
MILK 2.2
FLAX 1.9
CALVES 1.1
CHICKENS 1.1
HAY 1.0
LAMBS-SHEEP .4
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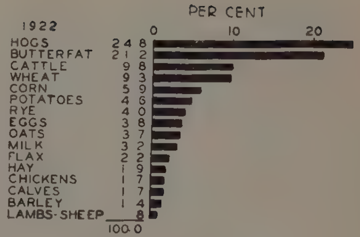
PER CENT
0
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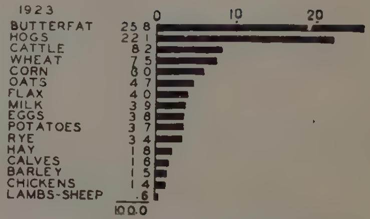
1922
HOGS 24.8
BUTTERFAT 21.2
CATTLE 9.8
WHEAT 9.3
CORN 5.9
POTATOES 4.6
RYE 4.0
EGGS 3.8
OATS 3.7
MILK 3.2
FLAX 2.2
HAY 1.9
CHICKENS 1.7
CALVES 1.7
BARLEY 1.4
LAMBS-SHEEP .8
100.0


0
10
20
1923
BUTTERFAT 25.8
HOGS 22.1
CATTLE 8.2
WHEAT 7.5
CORN 6.0
OATS 4.7
FLAX 4.0
MILK 3.9
EGGS 3.8
POTATOES 3.7
RYE 3.4
HAY 1.8
CALVES 1.6
BARLEY 1.5
CHICKENS 1.4
LAMBS-SHEEP .6
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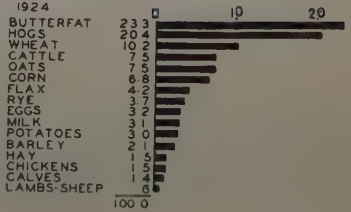
10
20
1924
BUTTERFAT 23.3
HOGS 20.4
WHEAT 10.2
CATTLE 7.5
OATS 7.5
CORN 6.8
FLAX 4.2
RYE 3.7
EGGS 3.2
MILK 3.1
POTATOES 3.0
BARLEY 2.1
HAY 1.5
CHICKENS 1.5
CALVES 1.4
LAMBS-SHEEP .6
100.0

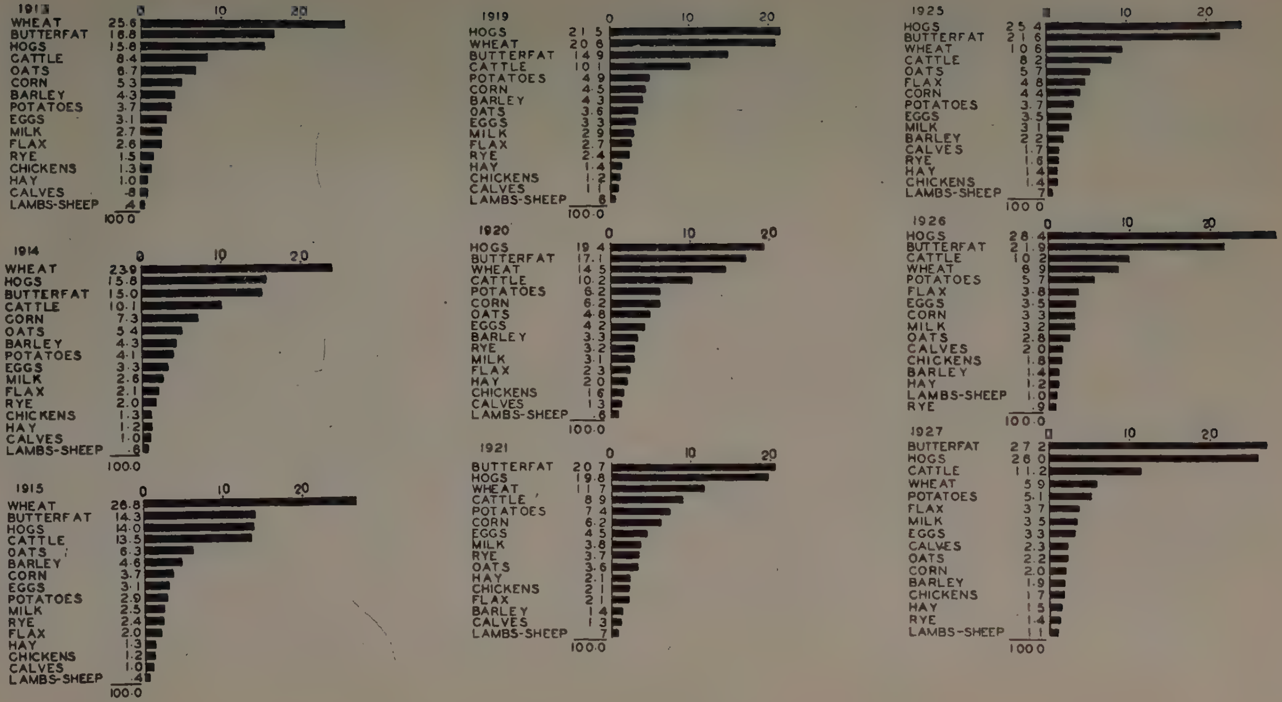

Fig. 7. Percentage of Total Annual Cash Income of Minnesota Farmers Received from Sales of Each of the Principal Products, 1910-1927

SOURCES OF PRICE AND QUANTITY DATA AND METHODS OF ESTIMATING AMOUNTS MARKETED

The following section is a detailed account of the data used, the sources from which they were taken, and the methods used for estimating the data in those instances in which they were inadequate for the purposes of the index series.

Wheat

The figures for the amount of wheat sold by the farmers of Minnesota have been derived by taking the official estimates of the annual production in the state, made by the United States Department of Agriculture, and deducting from this the amount necessary to plant the acreage of the following season. A seed requirement of one and one-half bushels per acre has been assumed. There should be some further deduction because of the amount wasted or fed to livestock. The Food Research Institute has estimated the amount of wheat wasted and fed at four-tenths of a bushel per capita.[12] On the basis of a population of 115,000,000 this would amount to 46,000,000 bushels for the entire United States, or approximately 6 per cent of a 750,000,000 bushel crop. A deduction on this account would reduce the estimates probably not more than 5 per cent. Because, however, a considerable portion of the waste occurs elsewhere than on the farm, and the amount fed includes purchases for feed after the producer has sold it, it seems incorrect to deduct from the marketings of farmers the entire amount of the waste and feed, and there is no basis for determining what portion of such a deduction properly belongs to the period when the wheat is in the hands of the farmer. No deduction on this account has therefore been made. Another source of error in the estimates of the amounts sold lies in the failure to allow for difference in carry-over from one crop year to the next. The carry-over varies from year to year and is dependent chiefly upon the size and quality of the preceding crop, the price at which it might be sold, and the prospect for the new crop. Absence of adequate data prevents adjustments from being made. A greater error might easily be introduced by attempting to adjust marketings for variations in the size of the carry-over than by assuming that a constant carry-over exists, as has been done in this study.

The production, amount necessary for planting in the following year, and total annual sales of wheat by the farmers of Minnesota, estimated as above outlined, for the crop years from 1910 to 1927, are given in Table 6.

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[12] Wheat Studies of the Food Research Institute, Vol. II, No. 7, June, 1926, p. 246.

Table 6

Production of Wheat, Seed Requirement, and Amount Sold by the Farmers of Minnesota, 1910-1927
(Bushels)

Crop year (August to July)	Production*	Seed requirement	Amount sold†
1910-11	64,000,000	6,525,000	57,475,000
1911-12	43,935,000	6,487,000	37,448,000
1912-13	67,038,000	6,300,000	60,738,000
1913-14	68,040,000	6,070,000	61,970,000
1914-15	42,975,000	6,240,000	36,735,000
1915-16	70,870,000	5,197,500	65,672,500
1916-17	26,410,000	4,420,500	21,989,500
1917-18	51,611,000	5,428,500	46,182,500
1918-19	75,792,000	5,797,500	69,994,500
1919-20	35,731,000	4,501,500	31,229,500
1920-21	28,168,000	3,556,500	24,611,500
1921-22	22,938,000	2,983,500	19,954,500
1922-23	27,276,000	2,760,000	24,516,000
1923-24	20,785,000	2,574,000	18,211,000
1924-25	37,863,000	3,394,500	34,468,500
1925-26	30,269,000	3,231,000	27,038,000
1926-27	24,811,000	2,716,500	22,094,500
1927-28	20,925,000	2,601,000	18,324,000

* U. S. Dept. of Agr. Yearbooks.

† For calendar year totals, see Table 8.

These annual amounts were sold ordinarily during the twelve months following the harvest, from August to July of the following year. As a guide to the monthly sales of these amounts by the farmers, percentage distributions by months, based on total receipts at the Minneapolis market during each twelve-month period from August to July, have been computed. These distributions were adopted rather than the estimated monthly percentage marketings published by the United States Department of Agriculture, which constitute an average for the entire United States. Altho receipts on the Minneapolis market include much wheat not raised in Minnesota, and altho some wheat raised in Minnesota is marketed elsewhere, the receipts at the Minneapolis market are doubtless a much better indicator of the monthly tendencies of Minnesota farmers to market their crops than a series for the United States as a whole.

The percentage distribution by months from 1910 to 1927, based on the total receipts at Minneapolis for each crop year period from August to July, inclusive, are shown in Table 7. The percentages shown for January to July, 1910, are based on receipts for the twelve months from August, 1909, to July, 1910.

Table 7

Monthly Percentage Marketings of Wheat, Based on Total Annual Receipts at Minneapolis for year August to July, 1910-1927*

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	10.6	8.8	8.6	8.0	8.4	8.5	5.4	6.6	7.1
February	9.6	5.0	8.0	6.5	8.4	6.0	7.1	5.3	4.3
March	9.4	6.9	7.3	7.9	8.4	3.8	7.5	9.2	4.0
April	4.8	5.1	4.2	5.0	5.4	3.1	4.6	8.2	4.7
May	4.6	5.5	3.9	4.0	3.4	5.2	4.5	6.5	6.2
June	5.4	5.7	3.6	4.7	3.1	4.9	4.9	4.4	6.4
July	4.7	5.7	3.0	3.3	4.2	4.5	5.1	2.3	3.2
August	10.3	7.0	6.9	6.5	7.8	3.3	7.9	7.7	12.5
September	14.3	14.6	10.8	15.7	18.6	11.6	13.2	14.1	15.7
October	12.8	14.5	14.2	12.9	15.9	14.1	13.6	17.8	17.9
November	8.9	13.5	14.0	11.9	10.6	14.7	13.6	15.0	7.9
December	11.0	11.8	14.7	11.7	11.1	17.2	9.2	9.5	15.1

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	3.5	8.4	7.6	7.0	11.0	5.3	8.7	7.0	5.9
February	4.8	5.4	6.2	6.4	4.7	7.0	4.9	5.7	6.2
March	7.0	5.3	6.2	6.3	7.7	7.0	5.4	5.2	6.1
April	4.6	4.7	6.2	4.3	5.1	3.3	3.1	4.4	4.4
May	4.2	5.1	5.5	5.0	3.8	4.6	3.2	4.0	5.4
June	3.3	5.0	8.1	5.1	4.6	5.6	4.9	4.2	6.0
July	3.5	5.7	6.7	5.4	3.7	5.1	5.2	7.5	5.6
August	11.2	6.8	13.6	8.3	10.2	8.0	11.6	13.3	10.3
September	12.8	11.8	15.1	14.7	15.3	18.9	18.0	17.4	21.5
October	15.1	13.8	16.3	12.3	13.7	17.4	10.6	13.9	17.1
November	9.9	12.2	7.8	10.4	13.6	11.4	10.0	8.5	7.5
December	11.4	8.9	7.7	13.7	9.3	8.9	11.8	7.3	6.3

* Computed from reports of the Minneapolis Chamber of Commerce and from an unpublished manuscript by Hutzel Metzger.

These percentage distributions for months were applied to the annual crop year amounts sold by Minnesota farmers (Table 6), to secure the actual amounts marketed in each month.[13] For example, the wheat sold from the 1925-26 crop, 27,038,000 bushels, was estimated to have been marketed during the period August, 1925, to July, 1926, according to the percentage distribution shown for each month in this period—11.6 per cent in August and 18 per cent in September, 1925, and finally 7.5 per cent in July, 1926. The amounts sold in the months from January to July, 1910, are percentages of the 1909-10 crop, the total of which is not shown.

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[13] At the time the Minnesota index number was constructed, in the spring of 1927, the total receipts of the various grains at Minneapolis for the year August, 1926, to July, 1927, were not available. Total marketings were, therefore, estimated on the basis of the receipts up to that time, and a preliminary percentage distribution computed on that basis for the months from August to December, 1926, in order that the approximate amounts sold could be determined for inclusion in the base period. The percentage distributions shown in the various tables for this period have been revised, but the difference was not sufficiently large to justify the work of changing the estimated number of bushels sold as used in the base period computations.

Table 8

Amount of Wheat Sold Monthly by the Farmers of Minnesota, 1910-1927 (Bushels)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	5,287,068	5,057,800	3,220,528	4,859,040	5,205,480	3,122,475	3,546,315	1,451,307	3,278,958
February	4,788,288	2,873,750	2,995,840	3,947,970	5,205,480	2,204,100	4,662,748	1,165,444	1,985,847
March	4,688,532	3,965,775	2,733,704	4,798,302	5,205,480	1,395,930	4,925,437	2,023,034	1,847,300
April	2,394,144	2,931,225	1,572,816	3,036,900	3,346,380	1,138,785	3,020,935	1,803,139	2,170,578
May	2,294,388	3,161,125	1,460,472	2,429,520	2,106,980	1,910,220	2,955,263	1,429,317	2,863,315
June	2,693,412	3,276,075	1,348,128	2,854,686	1,921,070	1,800,015	3,217,952	967,538	2,955,680
July	2,344,266	3,276,075	1,123,440	2,004,354	2,602,740	1,653,075	3,349,298	505,758	1,477,840
August	5,919,925	2,621,360	4,190,922	4,028,050	2,865,330	2,167,192	1,737,170	3,556,052	8,749,312
September	8,218,925	5,467,408	6,559,704	9,729,290	6,832,710	7,618,010	2,902,614	6,511,733	10,989,137
October	7,356,800	5,429,960	8,624,796	7,994,130	5,840,865	9,259,822	2,990,572	8,220,485	12,529,015
November	5,115,275	5,055,480	8,503,320	7,374,430	3,893,910	9,653,858	2,990,572	6,927,375	5,529,565
December	6,322,250	4,418,864	8,928,486	7,250,490	4,077,585	11,295,670	2,023,034	4,387,338	10,569,170
Total	57,423,273	47,534,897	51,262,156	60,307,162	49,104,010	53,219,092	38,321,910	38,948,520	64,945,717

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	2,449,808	2,623,278	1,870,474	1,396,815	2,696,760	965,183	2,998,760	1,892,660	961,808
February	3,359,736	1,686,393	1,525,913	1,277,088	1,152,252	1,274,770	1,688,957	1,541,166	1,013,448
March	4,899,615	1,655,164	1,525,913	1,257,134	1,887,732	1,274,770	1,861,299	1,405,976	994,083
April	3,219,747	1,467,786	1,525,913	858,044	1,250,316	600,963	1,068,524	1,189,672	716,514
May	2,939,769	1,592,705	1,353,633	997,725	931,608	837,706	1,102,992	1,081,520	877,892
June	2,309,819	1,561,475	1,993,531	1,017,680	1,127,736	1,019,816	1,688,957	1,135,596	981,173
July	2,449,808	1,780,081	1,648,971	1,077,543	907,092	928,761	1,792,362	2,027,850	910,167
August	3,497,704	1,673,582	2,713,812	2,034,828	1,857,522	2,757,480	3,136,408	3,448,060*	1,887,372
September	3,997,376	2,904,157	3,013,130	3,603,852	2,786,283	6,514,547	4,866,840	4,531,736	3,939,660
October	4,715,654	3,396,387	3,252,584	3,015,468	2,494,907	5,997,519	2,866,028	3,620,463	3,133,404
November	3,091,721	3,002,603	1,556,451	2,549,664	2,476,696	3,929,409	2,703,800	2,216,610	1,374,300
December	3,560,163	2,190,424	1,536,497	3,358,692	1,693,623	3,067,697	3,190,484	1,822,546	1,154,412
Total	40,490,920	25,534,035	23,516,822	22,444,533	21,262,527	29,168,576	28,965,411	25,913,855	17,944,233

* Explanation in Note 13 applies to August to December, 1926.

Sales of wheat computed by this method for each month in the period 1910-1927 are given in Table 8, which also shows the total for the calendar year.

The prices of wheat used in this study are the monthly farm prices for the 15th of the month reported by the United States Department of Agriculture. These are shown in Table 9.

Table 9

Monthly Farm Prices for Wheat Received by Producers in Minnesota,* 1910-1927

(Fifteenth of the month)
(Per bushel)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	$1.02	$0.94	$0.94	$0.74	$0.77	$1.16	$1.15	$1.55	$2.04
February	1.04	.91	0.94	.78	0.80	1.27	1.14	1.60	2.04
March	1.04	.86	0.96	.78	0.83	1.30	1.04	1.70	2.02
April	1.02	.87	1.00	.78	0.83	1.40	1.06	2.06	2.01
May	0.98	.88	1.04	.81	0.84	1.43	1.08	2.30	2.01
June	1.00	.88	1.04	.82	0.81	1.26	1.02	2.16	1.98
July	1.06	.88	0.98	.81	0.81	1.20	1.06	2.21	2.00
August	1.07	.90	0.90	.80	0.93	1.12	1.27	2.20	2.04
September	1.02	.94	0.82	.78	1.00	0.93	1.41	2.02	2.04
October	0.98	.97	0.80	.76	0.98	0.86	1.52	2.02	2.06
November	0.95	.95	0.76	.76	1.01	0.88	1.62	2.02	2.05
December	0.94	0.93	0.73	0.76	1.03	0.99	1.56	2.04	2.05

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	$2.06	$2.50	$1.38	$1.02	$1.04	$0.99	$1.55	$1.55	$1.26
February	2.06	2.38	1.36	1.18	1.04	1.00	1.64	1.49	1.26
March	2.08	2.34	1.32	1.28	1.06	1.01	1.60	1.42	1.24
April	2.26	2.57	1.16	1.31	1.07	0.98	1.34	1.40	1.19
May	2.37	2.70	1.12	1.32	1.07	1.00	1.45	1.41	1.27
June	2.30	2.59	1.18	1.25	1.00	1.04	1.50	1.45	1.33
July	2.33	2.40	1.13	1.15	0.92	1.15	1.40	1.49	1.31
August	2.22	2.23	1.08	1.02	0.94	1.22	1.51	1.40	1.29
September	2.10	2.14	1.10	0.93	1.00	1.11	1.38	1.26	1.19
October	2.19	1.95	1.08	0.94	1.02	1.28	1.29	1.28	1.13
November	2.38	1.54	0.98	0.98	0.98	1.32	1.34	1.29	1.09
December	2.49	1.34	0.96	1.04	0.97	1.43	1.51	1.27	1.10

* Prices 1910-25, U.S. Dept. of Agr. Statistical Bull. 15.
Prices 1926-27, current numbers of Crops and Markets.

Corn

The data include under this item only the amounts of corn which farmers sold for cash. To include the total crop at current market prices and also the livestock crop at current prices would result in serious duplication in the income and erroneous weighting in the indexes. Consequently only cash sales of corn are considered. The estimated amount of corn sold by the farmers of Minnesota is based on the total production for the state reported by the United States Department of Agriculture, and the percentage of the crop shipped out of the county where grown. These percentages were obtained for the most part from the series of publications of the United States Department of Agriculture—the present Crops and Markets and the publications which it superseded.[14] The amounts shipped out of the county do not represent wholly the total amounts marketed, because local cash sales are not included. In the aggregate, such local sales assume considerable importance, and the estimated amount of corn sold is, therefore, somewhat too small. No data are available with which to make the proper adjustment, and the figure derived from the percentage shipped out of the county where grown is, therefore, accepted as the approximate amount sold. These percentages vary considerably from year to year. Table 10 shows the total production, the percentage shipped out of county where grown, and the estimate on this basis of the amount of corn sold by the farmers of Minnesota in each crop year.

Table 10

Production of Corn, Percentage of Crop Shipped from County Where Grown, and Amount Sold by the Farmers of Minnesota, 1910-1927

Crop year (August to July)	Production*	Shipped from county†	Amount sold‡
	bu.	per cent	bu.
1910-11	66,708,000	25	16,677,000
1911-12	74,140,000	14	10,379,600
1912-13	78,177,000	15	11,726,550
1913-14	96,000,000	25	24,000,000
1914-15	91,000,000	26	23,660,000
1915-16	64,400,000	2	1,288,000
1916-17	87,100,000	12	10,452,000
1917-18	91,800,000	13	11,934,000
1918-19	111,200,000	14	15,568,000
1919-20	119,920,000	16	19,187,200
1920-21	123,300,000	22	27,126,000
1921-22	156,620,000	22	34,456,400
1922-23	131,307,000	18	23,635,260
1923-24	154,692,000	24	37,126,080
1924-25	124,065,000	17	21,091,050
1925-26	148,896,000	18	26,801,280
1926-27	147,662,000	10	14,766,200
1927-28	127,246,000	8	10,179,680

* Yearbooks U.S. Dept. of Agr.

† See Note 14.

‡ For calendar year totals, see Table 12.

The percentage distributions for the marketing of corn by months were derived from records of receipts of corn on the Chicago market, which were thought to be more representative than receipts at Minneapolis. Table 11 shows the percentage which the receipts of each month at Chicago were of the total receipts for the period from August to July, inclusive, of each crop year.

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[14] These percentages figures were available for the most part from records of the United States Department of Agriculture. If not, they were estimated by interpolation or other available information. In the most recent periods, preliminary estimates of this percentage figure made by the United States Department of Agriculture were used, and it is possible that slight revision may have occurred subsequently.

Table 11

Monthly Percentage Marketings of Corn, Based on Total Annual Receipts at Chicago for Year August to July, 1910-1927*

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	9.2	9.6	9.8	14.3	12.6	20.8	11.3	10.6	6.9
February	13.6	9.4	14.4	15.8	9.8	8.0	14.8	9.0	12.6
March	9.2	7.2	11.4	11.9	8.5	3.8	7.8	8.9	16.8
April	5.3	5.4	2.4	2.5	2.5	2.5	5.5	4.9	10.1
May	2.9	6.2	5.2	4.2	3.3	4.7	6.6	5.0	7.0
June	8.8	12.9	12.7	12.0	10.8	3.6	3.2	10.3	9.1
July	8.0	5.8	5.1	4.7	5.4	6.0	11.0	5.7	11.9
August	5.4	4.2	5.2	5.7	8.8	5.8	6.5	4.5	6.9
September	10.7	12.6	9.0	16.5	6.8	6.8	11.7	4.2	12.6
October	8.5	6.0	5.4	7.0	5.7	10.3	5.7	3.4	15.2
November	6.0	6.3	6.0	4.2	9.4	6.6	8.2	4.8	8.1
December	12.9	9.8	8.9	13.8	20.0	10.3	13.5	8.7	7.2

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	10.5	10.7	16.2	14.2	11.4	9.7	13.8	12.7	8.8
February	4.9	10.3	10.2	15.5	10.8	15.0	7.2	12.4	10.6
March	5.0	11.2	11.8	6.2	8.1	9.4	9.2	8.8	9.9
April	8.1	3.0	3.6	2.7	3.8	4.2	4.4	4.3	3.7
May	4.4	4.1	7.1	4.8	2.0	5.1	4.0	3.4	3.3
June	10.6	11.7	16.0	7.0	2.5	6.0	7.0	9.9	9.4
July	6.4	12.0	6.7	6.0	4.6	5.0	3.2	4.5	5.8
August	4.4	2.8	8.4	7.2	9.5	8.6	8.7	2.9	5.3
September	10.0	9.0	11.6	14.6	8.0	11.8	6.6	5.0	8.7
October	6.3	8.9	10.6	12.7	7.4	10.3	5.1	16.1	7.0
November	6.4	2.9	3.8	7.4	8.2	7.0	8.2	14.7	6.7
December	9.9	4.7	9.1	14.8	12.3	13.3	15.5	9.8	8.2

* Computed from records of the Chicago Board of Trade and from current reports of receipts as published in The Northwestern Miller.

These monthly percentage distributions were applied to the total crop year amounts estimated to have been sold by the farmers of Minnesota. The monthly sales of corn, computed on this basis, and totals for calendar years are given in Table 12.

Table 12

Amount of Corn Sold Monthly by the Farmers of Minnesota, 1910-1927 (Bushels)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	1,436,700	1,600,992	1,017,201	1,676,897	3,024,000	4,921,280	145,544	1,107,912	823,446
February	2,123,818	1,567,638	1,494,662	1,852,795	2,352,000	1,892,800	190,624	940,680	1,503,684
March	1,436,700	1,200,744	1,183,274	1,395,459	2,040,000	899,080	100,464	930,228	2,004,912
April	827,664	900,558	249,110	293,164	600,000	591,500	70,840	512,148	1,205,334
May	452,873	1,033,974	539,739	492,515	792,000	1,112,020	85,008	522,600	835,380
June	1,374,235	2,151,333	1,318,209	1,407,186	2,592,000	851,760	41,216	1,076,556	1,085,994
July	1,249,305	967,266	529,360	551,148	1,296,000	1,419,600	141,680	595,764	1,420,146
August	900,558	435,943	609,781	1,368,000	2,082,080	74,704	679,380	537,030	1,074,192
September	1,784,439	1,307,830	1,055,390	3,960,000	1,608,880	87,584	1,222,884	501,228	1,961,568
October	1,417,545	622,776	633,234	1,680,000	1,348,620	132,664	595,764	405,756	2,366,336
November	1,000,620	653,915	703,593	1,008,000	2,224,040	85,008	857,064	572,832	1,261,008
December	2,151,333	1,017,201	1,043,663	3,312,000	4,732,000	132,664	1,411,020	1,038,258	1,120,896
Total	16,155,790	13,460,170	10,377,216	18,997,164	24,691,620	12,200,664	5,541,488	8,740,992	16,662,896

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	1,634,640	2,053,030	4,394,412	4,892,809	2,694,420	3,601,230	2,910,565	3,403,763	1,239,784
February	762,832	1,976,282	2,766,852	5,340,742	2,552,608	5,568,912	1,518,556	3,323,359	1,493,542
March	778,400	2,148,966	3,200,868	2,136,297	1,914,456	3,489,852	1,940,377	2,358,513	1,392,039
April	1,261,008	575,616	976,536	930,323	898,140	1,559,295	928,006	1,152,455	522,015
May	684,992	786,675	1,925,946	1,653,907	472,705	1,893,430	843,642	911,244	464,013
June	1,650,208	2,244,902	4,340,160	2,411,948	590,881	2,227,565	1,476,374	2,653,327	1,319,537
July	996,352	2,302,464	1,817,442	2,067,384	1,087,222	1,856,304	674,914	1,206,058	819,273
August	844,237	759,528	2,894,338	1,701,739	3,526,978	1,813,830	2,331,711	457,752*	539,523
September	1,918,720	2,441,340	3,996,942	3,450,748	2,970,086	2,488,744	1,768,884	767,842	885,632
October	1,208,794	2,414,214	3,652,378	3,001,678	2,747,330	2,172,378	1,366,865	2,495,488	712,578
November	1,227,981	786,654	1,309,343	1,749,009	3,044,339	1,476,374	2,197,705	2,273,995	682,039
December	1,899,533	1,274,922	3,135,532	3,498,018	4,566,508	2,805,110	4,154,198	1,520,919	834,734
Total	14,867,697	19,764,593	34,410,749	32,834,602	27,065,673	30,953,024	22,111,797	22,524,715	10,904,709

* Explanation in Note 13 applies also to receipts at Chicago, August to December, 1926.

The prices of corn used in this study are the monthly farm prices for the 15th of the month, reported by the United States Department of Agriculture. These are shown in Table 13.

Table 13

Monthly Farm Prices for Corn Received by Producers in Minnesota,* 1910-1927

(Fifteenth of the month)

(Per bushel)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	$0.51	$0.42	$0.51	$0.36	$0.50	$0.58	$0.61	$0.82	$1.21
February	.52	.42	.50	.38	.50	.62	.60	0.88	1.29
March	.53	.42	.52	.40	.51	.62	.64	0.98	1.38
April	.49	.44	.58	.43	.53	.63	.70	1.20	1.40
May	.47	.46	.60	.47	.54	.64	.71	1.38	1.36
June	.49	.48	.59	.50	.56	.64	.73	1.47	1.33
July	.52	.53	.60	.51	.57	.66	.74	1.66	1.39
August	.54	.57	.60	.58	.63	.69	.76	1.70	1.40
September	.52	.56	.58	.62	.64	.66	.76	1.64	1.39
October	.47	.54	.52	.57	.58	.63	.75	1.57	1.26
November	.44	.54	.42	.53	.54	.62	.78	1.26	1.12
December	0.44	0.52	0.36	0.52	0.53	0.61	0.80	1.16	1.16

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	$1.15	$1.22	$0.48	$0.34	$0.56	$0.59	$0.94	$0.57	$0.58
February	1.10	1.24	.46	.40	.57	0.62	.92	.55	.59
March	1.18	1.30	.44	.44	.59	0.62	.85	.53	.56
April	1.34	1.44	.42	.46	.63	0.63	.80	.52	.55
May	1.43	1.54	.43	.48	.68	0.61	.84	.54	.65
June	1.46	1.56	.45	.48	.68	0.66	.94	.57	.78
July	1.57	1.40	.47	.49	.70	0.86	.93	.63	.83
August	1.62	1.28	.44	.50	.70	0.98	.95	.73	.90
September	1.40	1.13	.38	.49	.69	1.02	.85	.68	.85
October	1.18	0.82	.31	.50	.69	1.00	.65	.66	.76
November	1.16	0.60	.29	.54	.65	0.90	.61	.55	.66
December	1.19	0.50	0.32	0.56	0.58	0.91	0.55	0.56	0.68

* Prices 1910-25, U.S. Dept. of Agr. Statistical Bull. 15.
Prices 1926-27, current numbers of Crops and Markets.

Oats

The totals for the amounts of oats sold by the farmers of Minnesota were derived by the same general method and from the same sources as those used for corn. The production for each year, the percentage shipped out of the county where grown, and the actual amounts represented by these percentages, which are taken as the approximate crop year sales, are shown in Table 14.

The percentage distributions for the marketing of oats by months were based on the records of receipts on the Minneapolis market. Table 15 shows the percentage which the receipts of each month were of the total receipts for the crop year period from August to July, inclusive.

Table 14

Production of Oats, Percentage of Crop Shipped from County Where Grown, and Amount Sold by Farmers of Minnesota, 1910-1927

Crop year (August to July)	Production*	Shipped from county†	Amount sold‡
	bu.	per cent	bu.
1910-11	85,440,000	23	19,651,200
1911-12	67,214,000	20	13,442,800
1912-13	122,932,000	27	33,191,640
1913-14	124,644,000	28	34,900,320
1914-15	85,120,000	30	25,536,000
1915-16	138,675,000	35	48,536,250
1916-17	88,112,000	20	17,622,400
1917-18	120,250,000	26	31,265,000
1918-19	134,562,000	28	37,677,360
1919-20	98,728,000	20	19,745,600
1920-21	138,825,000	29	40,259,250
1921-22	99,480,000	23	22,880,400
1922-23	142,746,000	28	39,968,880
1923-24	153,254,000	27	41,378,580
1924-25	197,241,000	34	67,061,940
1925-26	200,340,000	31	62,105,400
1926-27	129,162,000	18	23,249,160
1927-28	116,580,000	18	20,984,400

* U.S. Dept. of Agr. Yearbook.

† See Note 14.

‡ For calendar year totals, see Table 16.

Table 15

Monthly Percentage Marketings of Oats, Based on Total Annual Receipts at Minneapolis for Year August to July, 1910-1927*

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	6.9	5.2	9.0	8.6	6.2	6.3	5.4	4.9	9.4
February	7.2	5.7	13.8	6.7	4.7	7.1	7.5	4.4	8.6
March	8.3	6.6	9.2	7.0	5.0	8.9	7.4	7.6	15.8
April	4.3	4.2	6.3	6.0	3.7	3.8	6.3	4.7	7.2
May	3.9	3.9	5.1	3.1	4.1	2.8	4.8	3.0	3.0
June	4.7	5.7	4.9	6.1	3.8	2.9	5.7	2.2	4.3
July	4.8	3.6	4.1	8.4	3.8	2.9	7.1	2.1	3.3
August	12.4	7.9	7.2	14.8	10.8	3.0	16.1	4.6	10.3
September	21.4	10.6	10.8	16.4	16.0	9.1	22.0	13.6	15.6
October	13.2	8.0	13.3	14.3	17.8	15.6	15.3	13.0	11.3
November	6.9	10.2	9.5	10.0	10.2	14.9	12.2	10.3	9.7
December	11.2	10.8	13.2	13.2	10.4	13.1	5.4	6.9	13.6

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	8.7	7.0	8.0	6.1	9.3	6.8	7.4	6.0	4.6
February	5.1	7.1	4.9	6.3	5.9	8.3	4.1	4.0	6.0
March	4.9	6.2	5.6	6.6	7.4	6.3	4.7	4.7	5.2
April	4.3	5.9	2.3	3.6	4.7	4.9	2.7	5.9	3.0
May	4.4	5.5	2.7	5.9	2.8	2.7	3.1	3.7	4.0
June	5.9	4.1	7.8	4.9	3.7	4.0	4.8	2.5	4.1
July	6.3	5.4	9.6	4.7	2.5	3.4	3.5	1.7	2.8
August	16.2	10.5	22.0	16.2	13.0	9.7	29.4	25.7	21.3
September	14.1	18.0	12.8	14.9	15.7	23.3	17.5	15.6	17.9
October	13.8	15.2	14.2	13.1	14.8	20.9	8.8	14.2	9.4
November	8.0	8.0	5.8	9.0	8.6	8.9	5.7	6.8	5.6
December	6.8	7.4	7.1	10.4	11.5	6.9	9.9	8.0	5.7

* Computed from records of the Minneapolis Chamber of Commerce.

Table 16

Amount of Oats Sold Monthly by the Farmers of Minnesota, 1910-1927 (Bushels)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	2,202,847	1,021,862	1,209,852	2,854,481	2,163,820	1,608,768	2,620,958	863,498	2,938,910
February	2,298,623	1,120,118	1,855,106	2,223,840	1,640,315	1,813,056	3,640,219	775,386	2,688,790
March	2,649,802	1,296,979	1,236,738	2,323,415	1,745,016	2,272,704	3,591,683	1,339,302	4,939,870
April	1,372,789	825,350	846,896	1,991,498	1,291,312	970,368	3,057,784	828,253	2,251,080
May	1,245,087	766,397	685,583	1,028,941	1,430,913	715,008	2,329,740	528,672	937,950
June	1,500,490	1,120,118	658,697	2,024,690	1,326,212	740,544	2,766,566	387,693	1,344,395
July	1,532,415	707,443	551,155	2,788,098	1,326,212	740,544	3,446,074	370,070	1,031,745
August	2,436,749	1,061,981	2,389,798	5,165,247	2,757,888	1,456,088	2,837,206	1,438,190	3,880,768
September	4,205,357	1,424,937	3,584,697	5,723,652	4,085,760	4,416,799	3,876,928	4,252,040	5,877,668
October	2,593,958	1,075,424	4,414,488	4,990,746	4,545,408	7,571,655	2,696,227	4,064,450	4,257,542
November	1,355,933	1,371,166	3,153,206	3,490,032	2,604,672	7,231,901	2,149,933	3,220,295	3,654,704
December	2,200,934	1,451,822	4,381,296	4,606,842	2,655,744	6,358,249	951,610	2,157,285	5,124,121
Total	25,594,984	13,243,597	24,967,509	39,211,482	27,573,272	35,895,684	33,964,928	20,225,134	38,927,543

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	3,277,930	1,382,192	3,220,740	1,395,704	3,717,106	2,813,743	4,962,584	3,726,324	1,138,744
February	1,921,545	1,401,938	1,972,703	1,441,465	2,358,164	3,434,422	2,749,540	2,484,216	1,484,040
March	1,846,191	1,224,227	2,254,518	1,510,106	2,957,697	2,606,851	3,151,911	2,918,954	1,285,679
April	1,620,126	1,164,990	925,963	823,694	1,878,537	2,027,550	1,810,672	3,664,219	742,020
May	1,657,804	1,086,008	1,087,000	1,349,944	1,119,129	1,117,222	2,078,920	2,297,900	991,809
June	2,222,964	809,570	3,140,221	1,121,140	1,478,849	1,655,143	3,218,973	1,552,635	1,013,849
July	2,373,674	1,066,262	3,864,888	1,075,379	999,222	1,406,872	2,347,168	1,055,792	690,593
August	3,198,787	4,227,221	5,033,688	6,474,959	5,379,215	6,505,008	18,258,988	5,812,290*	4,469,677
September	2,784,130	7,246,665	2,928,691	5,955,363	6,496,437	15,625,432	10,868,445	3,510,623	3,756,208
October	2,724,893	6,119,406	3,249,017	5,235,923	6,124,030	14,015,945	5,465,275	3,231,633	1,972,534
November	1,579,648	3,220,740	1,327,063	3,597,199	3,558,558	5,968,513	3,540,008	1,534,445	1,175,126
December	1,342,701	2,979,185	1,624,508	4,156,764	4,758,537	4,627,274	6,148,435	1,813,434	1,196,111
Total	26,550,393	31,928,404	30,629,000	34,137,660	40,825,481	61,803,975	64,600,919	33,602,465	19,916,390

* Explanation in Note 13 applies to August to December, 1926.

These monthly percentages applied to the total crop year amounts estimated to have been sold by the farmers of Minnesota result in the monthly sales of oats and the calendar year totals shown in Table 16.

The prices of oats used in this study are the 15th of the month prices paid to producers, reported by the United States Department of Agriculture. These are shown in Table 17.

Table 17

Monthly Farm Prices for Oats Received by Producers in Minnesota,* 1910-1927

(Fifteenth of the month)
(Per bushel)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	$0.38	$0.30	$0.42	$0.26	$0.32	$0.44	$0.40	$0.48	$0.72
February	.40	.30	.44	.26	.32	.48	.40	.50	.80
March	.40	.29	.46	.26	.32	.49	.37	.54	.84
April	.38	.30	.48	.27	.32	.50	.38	.62	.82
May	.36	.30	.49	.29	.32	.48	.38	.65	.74
June	.36	.33	.47	.32	.32	.46	.37	.64	.69
July	.39	.37	.42	.33	.32	.44	.37	.66	.68
August	.39	.38	.32	.34	.34	.40	.39	.60	.64
September	.35	.39	.26	.34	.39	.31	.40	.52	.62
October	.32	.40	.26	.32	.40	.28	.42	.54	.60
November	.32	.40	.26	.32	.40	.30	.46	.59	.60
December	0.31	0.40	0.26	0.32	0.40	0.34	0.46	0.66	0.62

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	$0.56	$0.74	$0.34	$0.25	$0.34	$0.36	$0.47	$0.33	$0.39
February	.52	.75	.32	.28	.34	.39	.45	.31	.39
March	.54	.78	.32	.29	.34	.38	.40	.31	.39
April	.60	.86	.28	.30	.36	.39	.35	.33	.38
May	.62	.92	.28	.30	.36	.39	.36	.33	.41
June	.60	.95	.29	.30	.34	.40	.42	.33	.43
July	.64	.84	.29	.27	.32	.45	.38	.33	.42
August	.64	.64	.25	.24	.30	.43	.33	.34	.41
September	.60	.53	.22	.24	.30	.40	.31	.31	.38
October	.59	.46	.22	.29	.32	.43	.29	.34	.39
November	.62	.39	.21	.32	.34	.40	.29	.35	.40
December	0.68	0.36	0.24	0.33	0.35	0.46	0.33	0.37	0.44

* Prices 1910-25, U.S. Dept. Agr. Statistical Bull. 15.
Prices 1926-27, current numbers of Crops and Markets.

Barley

The marketings of barley by Minnesota farmers were arrived at in the same general manner as those of corn and the other feed crops. The production of barley, the percentages shipped out of county where grown, and the actual amounts represented by these percentages, which are taken as the approximate crop year sales, are shown in Table 18.

Table 18

Production of Barley, Percentage of Crop Shipped from County Where Grown, and Amount Sold by Farmers of Minnesota, 1910-1927

Crop year (August to July)	Production*	Shipped from county†	Amount sold‡
	bu.	per cent	bu.
1910-11	26,985,000	..	13,398,000
1911-12	28,025,000	..	12,331,000
1912-13	42,018,000	..	18,487,920
1913-14	34,800,000	..	15,312,000
1914-15	31,694,000	56	17,748,640
1915-16	38,125,000	45	17,156,250
1916-17	26,125,000	49	12,801,250
1917-18	34,425,000	51	17,556,750
1918-19	31,694,000	45	14,262,300
1919-20	38,125,000	44	16,775,000
1920-21	22,378,000	40	8,951,200
1921-22	18,700,000	38	7,106,000
1922-23	24,062,000	38	9,143,560
1923-24	24,050,000	35	8,417,500
1924-25	29,280,000	45	13,176,000
1925-26	32,940,000	42	13,834,800
1926-27	32,675,000	30	9,802,500
1927-28	43,800,000	29	12,702,000

* U.S. Dept. of Agr. Yearbooks. † See Note 14. ‡ For calendar year totals, see Table 20.

Table 19

Monthly Percentage Marketings of Barley, Based on Combined Annual Receipts at Minneapolis and Milwaukee, for Year August to July, 1915-1926*

Month	1915	1916	1917	1918	1919	1920	1921
January	...	7.6	7.8	8.6	7.0	7.5	8.1
February	...	7.7	3.9	9.6	5.4	4.8	4.5
March	...	8.1	5.6	12.3	12.0	6.2	6.8
April	...	4.4	5.3	3.4	9.1	5.8	4.6
May	...	4.9	4.0	3.0	9.1	6.3	5.4
June	...	6.1	3.5	2.7	11.9	6.1	9.0
July	...	5.5	2.0	0.8	9.0	5.2	6.4
August	2.9	7.3	7.1	4.6	16.4	6.5	16.8
September	11.9	18.9	16.0	8.7	13.0	15.2	10.8
October	11.8	17.4	14.6	7.0	10.8	10.9	11.2
November	12.7	14.9	9.9	7.3	8.9	11.5	5.5
December	16.5	9.4	12.0	8.9	9.0	11.2	5.9

Month	1922	1923	1924	1925	1926	Average†
January	5.8	10.2	6.3	10.0	6.3	7.7
February	5.2	6.6	7.8	7.5	5.0	6.2
March	9.6	9.0	7.5	6.4	6.2	8.2
April	5.6	5.4	6.0	3.8	4.9	5.3
May	8.3	4.8	5.3	4.5	5.7	5.6
June	9.2	6.2	4.2	3.9	5.4	6.2
July	6.0	5.8	3.1	3.7	2.3	4.5
August	8.8	11.5	5.8	18.4	12.3	9.6
September	10.3	14.7	17.2	18.5	13.9	14.1
October	11.3	12.5	16.5	9.7	13.2	12.2
November	9.7	9.5	10.7	9.0	9.6	10.0
December	11.9	11.5	10.0	8.5	8.7	10.4

* Computed from records of the Minneapolis Chamber of Commerce and reports of receipts published in The Northwestern Miller.

† Average for 11 crop years, 1915-1926; August to December, 1926, not included.

Table 20

Amount of Barley Sold Monthly by the Farmers of Minnesota, 1910-1927 (Bushels)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	1,183,869	1,031,646	949,487	1,423,570	1,179,024	1,366,645	1,303,875	998,498	1,509,880
February	953,245	830,676	764,522	1,146,251	949,344	1,100,416	1,321,031	499,249	1,685,448
March	1,260,743	1,098,636	1,011,142	1,516,009	1,255,584	1,455,388	1,389,656	716,870	2,159,480
April	814,871	710,094	653,543	979,860	811,536	940,678	754,875	678,466	596,930
May	860,996	750,288	690,536	1,035,324	857,472	993,924	840,656	512,050	526,702
June	953,245	830,676	764,522	1,146,251	949,344	1,100,416	1,046,531	448,044	474,032
July	691,871	602,910	554,895	831,956	689,040	798,689	943,594	256,025	140,454
August	1,286,208	1,183,776	1,774,840	1,469,952	1,703,869	497,531	934,491	1,246,529	656,066
September	1,889,118	1,738,671	2,606,797	2,158,992	2,502,558	2,041,594	2,419,436	2,809,080	1,240,820
October	1,634,556	1,504,382	2,255,526	1,868,064	2,165,334	2,024,438	2,227,418	2,563,285	998,361
November	1,339,800	1,233,100	1,848,792	1,531,200	1,774,864	2,178,844	1,907,386	1,738,118	1,041,148
December	1,393,392	1,282,424	1,922,744	1,592,448	1,845,859	2,830,781	1,203,317	2,106,810	1,269,345
Total	14,261,914	12,797,279	15,797,346	16,699,877	16,683,828	17,329,344	16,292,266	14,573,024	12,298,666

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	998,361	1,258,125	725,047	412,148	932,643	530,302	1,317,600	871,592	879,049
February	770,164	805,200	402,804	369,512	603,475	656,565	988,200	691,740	700,751
March	1,711,476	1,040,050	608,682	682,176	822,920	631,312	843,264	857,758	688,311
April	1,297,869	972,950	411,755	397,936	493,752	505,050	500,688	677,905	501,721
May	1,297,869	1,056,825	483,365	589,798	438,891	446,128	592,920	788,584	443,671
June	1,697,214	1,023,275	805,608	653,752	566,901	353,535	513,864	747,079	733,923
July	1,283,607	872,300	572,877	426,360	530,326	260,942	487,512	318,200	199,030
August	2,751,100	581,828	1,193,808	804,633	968,013	764,208	2,545,603	1,205,708*	1,575,048
September	2,180,750	1,360,582	767,448	941,787	1,237,372	2,266,272	2,559,438	1,362,548	2,133,936
October	1,811,700	975,681	795,872	1,033,222	1,052,188	2,174,040	1,341,976	1,293,930	1,282,902
November	1,492,975	1,029,388	390,830	886,925	799,662	1,409,832	1,245,132	941,040	863,736
December	1,509,750	1,002,534	419,254	1,088,084	968,012	1,317,600	1,175,958	852,818	978,054
Total	18,802,835	11,978,738	7,577,350	8,286,333	9,414,155	11,315,786	14,112,155	10,608,902	10,980,132

* Explanation in Note 13 applies to August to December, 1926.

The percentage distributions for the marketing of barley by months were based on the combined receipts of barley at the Minneapolis and Milwaukee markets. Table 19 shows the percentage which the combined receipts for each month at the two markets constituted of the combined total receipts for the crop years from August to July, inclusive. The data on which to base these distributions were not available for the early years included in the index. An average of the percentage distributions for 1915 to 1926 has been substituted in these instances.

These percentage distributions, applied to the annual crop year marketings, result in monthly sales of barley and calendar year totals as shown in Table 20.

The prices of barley used in this study are the 15th of the month prices received by producers in Minnesota as reported by the United States Department of Agriculture. These prices are shown in Table 21.

Table 21

Monthly Farm Prices for Barley Received by Producers in Minnesota,* 1910-1927

(Fifteenth of the month)

(Per bushel)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	$0.53	$0.70	$0.96	$0.44	$0.46	$0.56	$0.58	$0.89	$1.34
February	.54	.72	0.98	.44	.47	.62	.60	0.94	1.55
March	.54	.78	0.98	.43	.46	.62	.56	0.99	1.73
April	.50	.88	1.00	.42	.44	.62	.58	1.13	1.62
May	.48	.86	0.99	.44	.44	.62	.60	1.20	1.32
June	.50	.81	0.87	.46	.42	.60	.60	1.10	1.04
July	.52	.80	0.67	.44	.41	.60	.59	1.14	0.96
August	.55	.82	0.49	.48	.48	.56	.66	1.16	0.89
September	.57	.88	0.43	.54	.52	.46	.74	1.10	0.82
October	.56	.94	0.45	.52	.49	.44	.78	1.14	0.78
November	.58	.96	0.44	.50	.52	.47	.84	1.11	0.78
December	0.64	0.95	0.42	0.46	0.52	0.51	0.86	1.22	0.78

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	$0.76	$1.28	$0.53	$0.38	$0.47	$0.49	$0.77	$0.52	$0.56
February	0.75	1.24	.48	.42	.47	.51	.76	.50	.57
March	0.80	1.26	.48	.44	.47	.54	.75	.49	.58
April	0.91	1.36	.46	.46	.48	.55	.70	.49	.60
May	0.98	1.42	.44	.47	.48	.58	.71	.51	.66
June	0.98	1.34	.45	.46	.48	.58	.71	.51	.75
July	1.03	1.14	.46	.44	.46	.62	.72	.52	.66
August	1.08	0.91	.42	.40	.44	.64	.62	.52	.62
September	1.04	0.79	.40	.40	.44	.63	.55	.48	.62
October	1.05	0.72	.38	.43	.45	.73	.51	.51	.63
November	1.12	0.66	.34	.46	.45	.67	.51	.52	.62
December	1.23	0.60	0.34	0.47	0.48	0.72	0.52	0.52	0.71

* Prices 1910-25, U.S. Dept. of Agr. Statistical Bull. 15.
Prices 1926-27, current numbers of Crops and Markets.

Rye

The amount of rye sold by the farmers of Minnesota was computed according to the methods outlined for wheat. The estimated amounts sold annually were derived by subtracting a seed allowance of one and one half bushels per acre for the acreage planted in the following year, from the annual production figure reported by the United States Department of Agriculture. This figure, when taken to represent annual sales has the same defect as the wheat estimate. In the case of rye the overestimate caused by not making an allowance for the amount fed and wasted, may be as high as 8 or 10 per cent. This estimate of error is higher than for wheat because more of the rye crop is fed on the farm. The production figures, amount necessary for seed, and estimated amount sold in each crop year are shown in Table 22.

Table 22

Production of Rye, Seed Requirement, and Amount Sold by Farmers of Minnesota, 1910-1927

(Bushels)

Crop year (August to July)	Production*	Seed requirement	Amount sold†
1910-11	4,352,000	360,000	3,992,000
1911-12	4,488,000	393,000	4,095,000
1912-13	6,026,000	450,000	5,576,000
1913-14	5,700,000	418,500	5,281,500
1914-15	5,245,000	450,000	4,795,000
1915-16	6,825,000	502,500	6,322,500
1916-17	5,250,000	615,000	4,635,000
1917-18	6,716,000	652,500	6,063,500
1918-19	8,700,000	783,000	7,917,000
1919-20	8,363,000	720,000	7,643,000
1920-21	8,806,000	960,000	7,846,000
1921-22	11,200,000	1,731,000	9,469,000
1922-23	21,926,000	1,368,000	20,558,000
1923-24	12,312,000	1,048,500	11,263,500
1924-25	14,718,000	672,000	14,046,000
1925-26	5,824,000	550,500	5,273,500
1926-27	5,940,000	613,500	5,326,500
1927-28	7,009,000	670,500	6,338,500

* U.S. Dept. of Agr. Yearbooks.

† For calendar year totals, see Table 24.

Table 23

Monthly Percentage Marketings of Rye, Based on Total Annual Receipts at Minneapolis for Year August to July, 1910-1927*

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	7.8	8.3	5.5	6.7	5.2	7.6	5.9	4.0	8.2
February	6.5	5.0	4.1	5.6	4.7	6.1	6.1	2.4	9.2
March	5.3	8.9	5.1	4.6	5.1	3.3	5.1	5.8	9.2
April	3.9	4.6	3.1	3.9	4.1	1.7	3.6	4.3	5.4
May	2.7	5.2	3.4	2.9	4.8	1.7	2.7	3.3	2.5
June	2.2	2.2	3.6	3.1	4.1	1.5	2.6	2.9	1.8
July	1.8	4.2	2.2	3.4	2.0	1.0	2.3	1.4	0.9
August	10.5	16.0	13.8	12.7	13.0	3.9	4.1	7.2	5.7
September	15.6	14.3	17.8	19.4	20.3	10.6	21.8	15.3	13.8
October	13.0	18.4	16.7	18.6	14.9	20.6	20.9	17.2	5.3
November	10.0	15.7	12.8	10.7	14.2	20.9	19.3	12.6	7.5
December	12.5	8.6	8.7	8.6	14.6	15.9	9.8	10.6	18.5

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	3.9	9.7	10.3	4.6	16.0	5.4	5.9	5.3	7.5
February	2.4	7.9	6.6	5.6	8.1	7.0	2.6	4.4	8.9
March	17.4	8.3	7.5	7.4	5.7	5.2	3.5	5.0	4.3
April	8.7	9.1	3.7	3.2	4.7	2.9	2.3	2.5	3.8
May	6.5	4.2	5.0	5.1	2.7	2.9	2.3	3.7	5.6
June	4.5	4.2	5.5	4.5	4.2	6.7	3.7	3.3	5.7
July	5.6	5.1	7.9	12.0	2.3	5.0	1.4	3.0	3.6
August	12.5	11.6	15.5	11.8	17.4	15.5	12.2	11.6	19.3
September	13.6	12.2	11.4	8.4	16.2	19.4	28.9	16.2	16.0
October	11.4	10.6	17.6	12.5	11.7	29.3	10.6	12.3	12.1
November	6.7	7.3	5.1	8.2	9.2	8.8	9.5	9.1	7.7
December	7.2	11.8	7.9	15.5	10.4	5.3	11.6	11.4	5.5

* Computed from records of the Minneapolis Chamber of Commerce.

The percentage distributions for the marketing of rye were based on receipts at the Minneapolis market. The percentages which the receipts for each month constituted of the total receipts for the crop year August to July are shown in Table 23.

When the percentage distributions are applied to the annual amounts sold in each crop year, monthly sales and calendar year totals of the amounts shown in Table 24 result.

The prices of rye used in this study are the 15th of the month prices paid to producers, reported by the United States Department of Agriculture. These are shown in Table 25.

Table 24

Amount of Rye Sold Monthly by the Farmers of Minnesota, 1910-1927 (Bushels)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	314,855	331,336	225,225	373,592	274,638	364,420	373,028	185,400	497,207
February	262,379	199,600	167,895	312,256	248,231	292,495	385,672	111,240	557,842
March	213,940	355,288	208,845	256,496	269,356	158,235	322,448	268,830	557,842
April	157,427	183,632	126,945	217,464	216,542	81,515	227,610	199,305	327,429
May	108,988	207,584	139,230	161,704	253,512	81,515	170,708	152,955	151,588
June	88,805	87,824	147,420	172,856	216,542	71,925	164,385	134,415	109,143
July	72,659	167,664	90,090	189,584	105,630	47,950	145,417	64,890	54,572
August	419,160	655,200	769,488	670,750	623,350	246,578	190,035	436,572	451,269
September	622,752	585,585	992,528	1,024,611	973,385	670,185	1,010,430	927,715	1,092,546
October	518,960	753,480	931,192	982,359	714,455	1,302,435	968,715	1,042,922	419,601
November	399,200	642,915	713,728	565,121	680,890	1,321,403	894,555	764,001	593,775
December	499,000	352,170	485,112	454,209	700,070	1,005,278	454,230	642,731	1,464,645
Total	3,678,125	4,522,278	4,997,698	5,381,002	5,276,601	5,643,934	5,307,232	4,930,976	6,277,459

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	308,763	741,371	808,138	435,574	3,289,280	608,229	828,714	279,496	469,039
February	190,008	603,797	517,836	530,264	1,665,198	788,445	365,196	232,034	557,910
March	1,377,558	634,369	588,450	700,706	1,171,806	585,702	491,610	263,675	269,080
April	688,779	695,513	290,302	303,008	966,226	326,642	323,058	131,838	236,988
May	514,605	321,006	392,300	482,919	555,066	326,642	323,058	195,120	353,014
June	356,265	321,006	431,530	426,105	863,436	754,654	519,702	174,026	357,951
July	443,352	389,793	619,834	1,136,280	472,834	563,175	196,644	158,205	224,645
August	955,375	910,136	1,467,695	2,425,844	1,959,849	2,177,130	643,367	546,034*	1,223,330
September	1,039,448	957,212	1,079,466	1,726,872	1,824,687	2,724,924	1,524,042	766,209	1,014,160
October	871,302	831,676	1,666,544	2,569,750	1,317,830	4,115,478	558,991	576,859	766,958
November	512,081	572,758	482,919	1,685,756	1,036,242	1,236,048	500,983	431,543	488,064
December	550,296	925,828	748,051	3,186,490	1,171,404	744,438	611,726	537,227	348,617
Total	7,807,832	7,904,465	9,093,065	15,609,568	16,293,858	14,951,507	6,887,091	4,292,266	6,309,756

* Explanation in Note 13 applies to August to December, 1926.

Table 25

Monthly Farm Prices for Rye Received by Producers in Minnesota,* 1910-1927

(Fifteenth of the month)

(Per bushel)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	$0.65	$0.70	$0.82	$0.48	$0.48	$1.00	$0.86	$1.24	$1.76
February	.66	.70	.81	.50	.48	1.06	0.86	1.28	1.98
March	.66	.72	.80	.50	.50	1.04	0.82	1.36	2.38
April	.65	.74	.80	.50	.50	1.02	0.81	1.56	2.51
May	.64	.78	.80	.52	.50	1.03	0.82	1.88	2.12
June	.64	.79	.76	.51	.50	1.01	0.84	1.98	1.74
July	.66	.75	.68	.50	.50	0.96	0.83	1.84	1.62
August	.66	.74	.58	.52	.62	0.88	0.92	1.65	1.58
September	.66	.77	.54	.53	.76	0.82	1.05	1.63	1.52
October	.64	.80	.54	.50	.78	0.82	1.12	1.68	1.47
November	.64	.80	.52	.48	.84	0.84	1.22	1.66	1.48
December	0.66	0.79	0.49	0.48	0.92	0.82	1.24	1.69	1.48

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	$1.42	$1.52	$1.27	$0.67	$0.70	$0.56	$1.32	$0.88	$0.82
February	1.32	1.44	1.27	.76	.68	0.58	1.34	.80	.87
March	1.36	1.46	1.20	.84	.67	0.54	1.26	.71	.86
April	1.50	1.69	1.12	.86	.68	0.51	0.97	.71	.84
May	1.45	1.78	1.10	.87	.66	0.52	1.02	.69	.91
June	1.32	1.82	1.08	.80	.56	0.55	1.02	.75	.96
July	1.36	1.74	0.98	.68	.50	0.63	0.86	.84	.91
August	1.38	1.65	0.90	.58	.51	0.77	0.91	.85	.79
September	1.31	1.64	0.85	.54	.53	0.77	0.75	.79	.80
October	1.26	1.52	0.75	.58	.55	1.09	0.65	.80	.79
November	1.26	1.34	0.64	.64	.54	1.12	0.65	.80	.84
December	1.42	1.22	0.64	0.69	0.54	1.17	0.86	0.78	0.88

* Prices 1910-25, U.S. Dept. of Agr. Statistical Bull. 15.
Prices 1926-27, current numbers of Crops and Markets.

Flax

The quantity of flax sold has been estimated from the annual production reported for the state by the United States Department of Agriculture, minus a seed allowance of one-half bushel per acre for the acreage planted in the following year. The assumption that sales of flax equal the total production less the seed requirement is valid in this case, because no flax is used on farms for feeding purposes. The figures for production, seed allowance, and sales by crop years are shown in Table 26.

The monthly percentage distributions for flax computed on the basis of the receipts at Minneapolis for the crop year August to July, are shown in Table 27.

The estimated amounts sold by months and the calendar year totals which result when these percentages are applied to the annual crop year marketings are shown in Table 28.

Table 26

Production of Flax, Seed Requirement, and Amount Sold by the Farmers of Minnesota, 1910-1927

(Bushels)

Crop year (August to July)	Production*	Seed requirement	Amount sold†
1910-11	2,828,000	200,000	2,628,000
1911-12	3,200,000	202,000	2,998,000
1912-13	4,121,000	175,000	3,946,000
1913-14	3,150,000	157,500	2,992,500
1914-15	2,930,000	150,000	2,780,000
1915-16	3,150,000	137,500	3,012,500
1916-17	1,700,000	110,000	1,590,000
1917-18	2,090,000	150,000	1,940,000
1918-19	3,536,000	160,000	3,376,000
1919-20	2,304,000	160,000	2,144,000
1920-21	3,040,000	157,000	2,883,000
1921-22	2,983,000	155,000	2,828,000
1922-23	3,100,000	263,500	2,836,500
1923-24	5,270,000	356,000	4,914,000
1924-25	8,117,000	370,000	7,747,000
1925-26	7,400,000	455,000	6,945,000
1926-27	7,652,000	378,500	7,273,500
1927-28	7,343,000	363,000	6,980,000

* U.S. Dept. of Agr. Yearbooks.

† For calendar year totals, see Table 28.

Table 27

Monthly Percentage Marketings of Flax, Based on Total Annual Receipts at Minneapolis for Year August to July, 1910-1927*

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	9.7	4.2	6.2	11.8	8.9	8.3	4.3	6.3	8.6
February	6.7	5.4	5.3	10.2	6.0	6.2	5.4	5.1	9.0
March	8.3	4.1	4.6	8.6	7.4	5.3	11.0	5.1	8.5
April	4.4	2.0	5.4	6.1	3.4	2.0	6.6	4.5	4.6
May	2.2	2.1	6.6	4.2	1.7	1.1	6.0	3.0	5.7
June	1.6	2.2	5.1	4.2	2.1	2.0	5.0	6.6	10.5
July	1.2	2.4	5.7	3.5	2.9	3.3	6.0	3.8	3.4
August	2.4	2.2	1.3	3.5	1.6	1.6	2.3	1.5	1.3
September	15.2	6.6	5.7	9.5	12.5	4.7	3.7	4.3	7.1
October	27.3	14.1	13.5	21.2	26.2	14.1	27.7	15.9	12.2
November	23.1	18.2	12.4	18.9	17.3	20.4	19.7	18.0	11.4
December	9.5	19.9	18.3	14.3	14.1	15.1	12.2	10.0	10.5

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	7.4	6.5	4.1	6.8	7.1	3.7	8.7	3.3	4.7
February	6.3	6.9	3.9	4.6	4.0	2.6	5.2	2.4	3.6
March	11.0	8.1	6.2	5.8	5.1	2.4	4.7	2.8	3.1
April	5.8	3.1	6.4	4.7	7.6	2.2	2.6	3.2	1.9
May	5.8	5.9	8.5	6.7	6.4	3.0	2.8	3.8	2.9
June	12.5	9.9	7.8	4.9	7.6	3.0	3.1	2.3	3.1
July	8.6	10.5	5.0	3.5	5.7	2.7	2.0	2.6	1.6
August	3.7	4.4	7.2	5.0	10.5	1.9	9.7	9.3	3.3
September	14.3	9.6	12.4	15.0	27.3	15.8	29.4	17.3	33.3
October	10.9	21.8	27.0	17.0	20.1	24.2	24.3	32.6	29.1
November	10.8	11.9	8.7	9.5	13.5	19.4	9.8	12.4	8.0
December	9.4	10.5	7.9	10.0	9.0	9.6	6.4	7.5	3.7

* Computed from records of the Minneapolis Chamber of Commerce.

Table 28

Amount of Flax Sold Monthly by the Farmers of Minnesota, 1910-1927 (Bushels)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	299,585	110,376	185,876	465,628	266,333	230,740	129,538	100,170	166,840
February	206,930	141,912	158,894	402,492	179,550	172,360	162,675	81,090	174,600
March	256,346	107,748	137,908	339,356	221,445	147,340	331,375	81,090	164,900
April	135,894	52,560	161,892	240,706	101,745	55,600	198,825	71,550	89,240
May	67,947	55,188	197,868	165,732	50,873	30,580	180,750	104,940	110,580
June	49,416	57,816	152,898	165,732	62,843	55,600	150,625	104,940	203,700
July	37,062	63,072	170,886	138,110	86,782	91,740	180,750	60,420	65,960
August	63,072	65,956	51,298	104,737	44,480	48,200	36,570	29,100	43,888
September	399,456	197,868	224,922	284,288	347,500	141,587	58,830	83,420	239,696
October	717,444	422,718	532,710	634,410	728,360	424,763	440,430	308,460	411,872
November	607,068	545,636	489,304	565,583	480,940	614,550	313,230	349,200	384,864
December	249,660	596,602	722,118	427,927	391,980	454,886	193,980	194,000	354,480
Total	3,089,880	2,417,452	3,186,574	3,934,701	2,962,831	2,467,946	2,377,578	1,511,140	2,410,620

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	249,824	139,360	118,203	192,304	201,391	181,818	673,989	229,185	326,322
February	212,688	147,936	112,437	130,088	113,460	127,764	402,844	166,680	249,455
March	371,360	173,664	178,746	164,024	144,662	117,936	364,109	194,460	214,647
April	195,808	66,464	184,512	132,916	215,574	108,108	201,422	222,240	131,979
May	195,808	126,496	245,055	189,476	181,536	147,420	216,916	263,910	201,594
June	422,000	212,256	224,874	138,572	215,574	147,420	240,157	159,735	214,647
July	290,336	225,120	144,150	98,980	161,681	132,678	154,940	180,570	111,674
August	79,328	126,852	203,616	141,825	515,970	147,193	673,665	688,415*	230,340
September	306,592	276,768	350,672	425,475	1,341,522	1,224,026	2,041,830	1.271,543	2,324,340
October	233,696	628,494	763,560	482,205	987,714	1,874,774	1,687,635	2,397,304	2,031,180
November	231,552	343,077	246,036	269,468	663,390	1,502,918	680,610	915,187	558,400
December	201,536	302,715	223,412	283,650	442,260	743,712	444,480	550,732	258,260
Total	2,990,526	2,769,202	2,995,273	2,648,983	5,184,734	6,455,766	7,782,597	7.239,961	6,852,838

* Explanation in Note 13 applies to August to December, 1926.

The prices of flax used in this study are the 15th of the month prices paid to producers, reported by the United States Department of Agriculture. These are shown in Table 29.

Table 29

Monthly Farm Prices for Flax Received by Producers in Minnesota,* 1910-1927

(Fifteenth of the month)
(Per bushel)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	$1.82	$2.30	$1.93	$1.11	$1.31	$1.54	$2.00	$2.55	$3.24
February	1.92	2.40	1.89	1.16	1.34	1.66	2.12	2.56	3.43
March	1.92	2.38	1.88	1.16	1.36	1.66	2.10	2.60	3.66
April	2.04	2.38	1.94	1.14	1.37	1.70	1.99	2.83	3.82
May	2.07	2.34	1.99	1.15	1.38	1.74	1.84	3.01	3.73
June	1.94	2.13	1.98	1.15	1.40	1.66	1.72	2.92	3.52
July	2.04	1.95	1.82	1.18	1.48	1.53	1.74	2.82	3.83
August	2.21	1.97	1.68	1.25	1.50	1.50	1.87	2.91	4.05
September	2.32	2.08	1.58	1.28	1.38	1.50	1.94	3.08	3.87
October	2.34	2.12	1.43	1.25	1.25	1.58	2.15	3.06	3.62
November	2.30	1.98	1.28	1.23	1.24	1.72	2.36	2.96	3.40
December	2.26	1.87	1.14	1.26	1.34	1.82	2.48	3.06	3.36

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	$3.19	$4.56	$1.64	$1.74	$2.35	$2.20	$2.80	$2.29	$1.97
February	3.18	4.71	1.58	2.02	2.51	2.30	2.80	2.22	2.00
March	3.39	4.64	1.52	2.24	2.65	2.25	2.70	2.08	1.97
April	3.56	4.48	1.40	2.32	2.85	2.20	2.55	2.11	1.99
May	3.76	4.28	1.44	2.42	2.80	2.30	2.60	2.11	2.09
June	4.18	3.82	1.54	2.38	2.50	2.20	2.52	2.08	2.08
July	4.89	3.17	1.54	2.22	2.30	2.20	2.32	2.13	2.02
August	5.18	2.87	1.68	1.99	2.15	2.16	2.30	2.20	2.08
September	4.62	2.90	1.69	1.89	2.13	2.00	2.30	2.18	2.01
Oct.	4.04	2.68	1.60	2.06	2.16	2.14	2.37	2.01	1.96
November	4.18	2.14	1.50	2.18	2.14	2.30	2.33	1.99	1.90
December	4.42	1.74	1.58	2.23	2.27	2.50	2.37	2.00	1.90

* Prices 1910-25, U.S. Dept. of Agr. Statistical Bull. 15.
Prices 1926-27, current numbers of Crops and Markets.

Hay

The amount of hay sold by the farmers of Minnesota has been based on the percentage of the crop sold, as reported by the census for 1909 and 1919. For these years 4.6 and 6.1 per cent, respectively, were reported. In order to estimate the amount of the crop sold in the intervening years, straight-line interpolation has been applied to these percentages. For the years 1922, 1923, and 1924, the United States Department of Agriculture has reported that 8 per cent of the hay crop was shipped out of the county where grown. No estimate has been made since 1924 and an amount of 8 per cent has, therefore, been used for the years 1920 to 1927. The total production and the amount of sales estimated in this way are given in Table 30.

Table 30

Production of Hay, Percentage and Amount of Crop Sold by the Farmers of Minnesota, 1910-1927

Crop year (August to July)	Production*	Percentage sold	Amount sold†
	Tons		Tons
1909-10	....	4.6‡	......
1910-11	3,189,000	4.8	153,072
1911-12	2,974,000	4.9	145,726
1912-13	4,707,000	5.1	240,006
1913-14	4,613,000	5.2	239,876
1914-15	6,073,000	5.4	327,942
1915-16	5,812,000	5.5	319,660
1916-17	6,384,000	5.7	563,888
1917-18	5,192,000	5.8	301,136
1918-19	4,685,000	6.0	281,100
1919-20	6,746,000	6.1‡	411,506
1920-21	5,884,000	8.0	470,720
1921-22	5,639,000	8.0	451,120
1922-23	5,639,000	8.0§	451,120
1923-24	4,869,000	8.0	389,520
1924-25	6,319,000	8.0	505,520
1925-26	6,227,000	8.0	498,160
1926-27	4,233,000	8.0	338,640
1927-28	7,906,000	8.0	632,480

* U.S. Dept. of Agr. Yearbooks.

† For calendar year totals, see Table 32.

‡ 14th Census—Agriculture, vol. V, p. 722.

§ Percentage shipped from county where grown, reported in Crops and Markets.

The distribution of sales of hay by months has been based on the percentage which the receipts for each month at Minneapolis constituted of the total receipts of the crop year from August to July. These percentage distributions are shown in Table 31.

These distributions were applied to the annual crop year sales, and the amounts found for each month together with calendar year totals are shown in Table 32.

The United States Department of Agriculture has reported the 15th-of-the-month price for five classes of hay, namely, alfalfa, timothy, clover, prairie, and loose, since October, 1914. For this period an unweighted average of all five quotations for a given month has been taken as the general price of hay received by Minneapolis producers. For the period prior to October, 1914, the department reported the price of loose hay only. For the period before October, 1914, monthly prices for hay of all kinds were estimated as follows: The ratio between the quotations for loose hay and the monthly average of the prices of the five classes of hay was computed for each month in the period 1915 to 1917. The average of these ratios for each calendar month was calculated and applied to the monthly quotations for loose hay from 1910 to October, 1914, in order to obtain monthly quotations for this period, which would correspond to the general hay quotations computed for subsequent years. The hay prices derived by these methods are shown in Table 33.

Table 31

Monthly Percentage Marketings of Hay, Based on Total Annual Receipts at Minneapolis for Year August to July, 1910-1927*

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	6.7	6.6	11.0	10.1	8.8	8.9	4.5	7.2	12.2
February	8.5	14.4	14.7	9.3	7.2	6.7	8.5	8.8	9.9
March	8.5	11.2	14.0	8.1	10.0	9.2	9.9	10.2	13.7
April	6.5	7.9	9.8	5.2	5.2	8.0	5.4	6.9	5.0
May	7.2	7.7	7.0	5.0	5.3	8.6	8.7	5.4	4.9
June	6.3	3.9	5.4	7.0	6.4	7.3	9.2	8.2	5.4
July	11.0	3.8	2.9	5.1	8.9	2.5	4.6	5.7	5.2
August	9.3	4.8	9.2	5.8	8.2	10.9	5.2	4.9	6.8
September	7.0	4.8	10.2	5.2	8.2	6.5	8.8	6.2	7.8
October	9.3	6.7	11.1	12.3	11.8	8.3	12.2	10.9	8.0
November	6.4	7.8	11.0	12.7	10.0	11.5	12.6	11.3	6.9
December	12.4	11.1	8.6	12.2	10.7	12.0	8.7	10.4	10.6

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	10.2	10.7	13.2	9.8	10.6	8.7	11.5	10.8	15.8
February	13.0	11.0	9.0	9.4	8.4	10.0	9.5	8.9	12.1
March	10.1	8.5	10.2	10.9	12.3	13.2	10.4	8.0	14.6
April	5.8	6.0	7.6	8.2	5.9	7.3	7.8	6.3	6.2
May	10.0	9.3	5.8	6.4	6.7	5.4	5.8	7.9	7.9
June	4.9	5.3	5.3	4.9	5.9	6.5	5.0	7.2	3.5
July	6.0	6.5	4.0	9.3	9.0	6.8	7.4	6.2	1.9
August	5.6	8.2	8.1	7.5	6.0	6.2	7.9	5.5	5.2
September	10.4	6.0	6.3	7.9	6.1	5.8	4.6	5.6	3.5
October	10.6	9.2	11.0	8.6	9.6	12.5	8.2	9.2	11.1
November	6.9	9.6	6.7	8.0	9.2	8.6	12.9	8.7	7.7
December	9.2	12.0	9.1	9.1	11.1	9.6	11.1	9.0	7.2

* Computed from records of the Minneapolis Chamber of Commerce.

Table 32

Amount of Hay Sold Monthly by the Farmers of Minnesota, 1910-1927 (Tons)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	17,355	10,103	16,030	24,246	21,109	29,187	14,385	26,200	36,739
February	22,017	22,042	21,422	22,325	17,271	21,972	27,171	32,022	29,812
March	22,017	17,144	20,402	19,445	23,988	30,171	31,646	37,117	41,256
April	16,837	12,093	14,281	12,483	12,474	26,235	17,262	25,108	15,057
May	18,650	11,787	10,201	12,003	12,713	28,203	27,810	19,650	14,756
June	16,319	5,970	7,869	16,804	15,352	23,940	29,409	29,839	16,261
July	28,493	5,817	4,226	12,243	21,349	8,199	14,704	20,742	15,659
August	14,236	6,995	22,085	13,913	26,891	34,843	18,922	14,756	19,115
September	10,715	6,995	24,486	12,474	26,891	20,778	32,022	18,670	21,926
October	14,236	9,764	26,646	29,505	38,697	26,532	44,394	32,824	22,488
November	9,797	11,367	26,406	30,464	32,794	36,761	45,850	34,028	19,396
December	18,981	16,176	20,645	29,265	35,090	38,359	31,658	31,318	29,797
Total	209,653	136,253	214,699	235,170	284,619	325,180	335,233	322,274	282,262

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	28,672	44,031	62,135	44,210	47,819	33,888	58,135	53,801	53,971
February	36,543	45,266	42,364	42,405	37,894	38,952	48,024	44,336	41,272
March	28,391	34,978	48,013	49,172	55,488	51,417	52,574	39,853	49,738
April	16,304	24,690	35,775	36,992	26,616	28,435	39,431	31,384	21,165
May	28,110	38,270	27,302	28,872	30,225	21,034	29,320	39,355	26,880
June	13,774	21,810	24,948	22,105	26,616	25,319	25,276	35,868	11,852
July	16,866	26,748	18,829	41,954	40,601	26,487	37,408	30,886	6,772
August	23,044	38,599	36,541	33,834	23,371	31,342	39,355	18,625*	32,889
September	42,797	28,243	28,421	35,638	23,761	29,320	22,915	18,625	22,137
October	43,620	43,306	49,623	38,796	37,394	63,190	40,849	30,478	70,205
November	28,394	45,189	30,225	36,090	35,836	43,475	64,263	28,784	48,701
December	37,859	56,486	41,052	41,052	43,237	48,530	55,296	30,478	45,539
Total	344,374	447,616	445,228	451,120	428,858	441,389	512,846	402,473	431,121

* Explanation in Note 13 applies to August to December, 1926.

Table 33

Monthly Farm Prices for Hay Received by Producers in Minnesota,* 1910-1927
(Fifteenth of the month)
(Per ton)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	$ 7.93	$12.61	$14.45	$ 8.06	$ 7.87	$ 8.32	$ 8.48	$ 8.40	$16.00
February	7.74	12.30	13.44	7.38	7.74	8.44	8.30	8.74	16.06
March	7.25	11.70	12.29	7.25	7.72	8.40	8.82	9.12	15.72
April	6.61	11.69	12.60	7.41	7.47	8.70	8.92	10.18	14.80
May	6.56	12.08	12.71	7.48	8.11	8.82	9.60	10.74	14.22
June	7.91	12.57	11.92	7.79	8.50	8.72	9.92	10.76	14.06
July	10.74	13.22	9.97	7.61	7.57	8.72	8.51	10.34	13.58
August	12.19	13.28	7.59	7.30	7.68	8.18	7.86	10.08	13.64
September	12.27	13.10	7.20	7.67	7.42	8.16	7.98	11.30	15.54
October	11.84	12.55	7.85	7.74	8.26	8.18	8.12	12.90	15.16
November	10.62	12.60	7.51	7.40	8.06	7.42	8.16	13.20	15.82
December	11.17	13.69	7.66	7.78	8.06	7.80	8.08	13.56	16.90

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	$16.78	$17.58	$13.06	$10.10	$11.14	$12.46	$10.94	$11.18	$15.48
February	17.58	18.30	11.98	10.56	10.68	12.60	10.86	10.96	16.90
March	17.82	18.10	11.28	10.40	11.06	10.22	11.72	11.34	16.70
April	19.72	18.50	10.76	10.76	11.56	12.00	11.68	11.20	16.70
May	21.64	19.78	11.12	10.96	12.42	11.90	11.28	11.42	17.12
June	22.16	18.58	10.22	10.66	12.16	11.82	11.40	11.52	15.50
July	17.98	17.32	10.42	10.54	11.52	11.84	10.72	12.78	11.90
August	16.74	16.28	10.08	11.08	11.46	11.96	10.56	13.20	10.60
September	16.10	15.86	10.06	9.92	11.70	12.22	10.72	13.24	10.12
October	15.94	15.12	10.06	10.16	12.66	11.58	10.46	14.48	9.48
November	16.32	14.49	10.06	10.42	12.68	12.04	10.40	14.62	8.98
December	17.80	13.78	10.02	10.92	12.58	11.52	11.60	15.46	9.28

* U.S. Dept. of Agr. Statistical Bull. 15 and current numbers of Crops and Markets. Unweighted average based on prices of alfalfa, clover, timothy, prairie, and loose hay, reported by U.S. Dept. of Agr., October, 1914-1927. Price previous to October, 1914, estimated as explained in text.

Potatoes

Data on potatoes consist chiefly of records of annual production and monthly car-load shipments by states. Figures of car-load shipments are available for Minnesota since July, 1917. Sales of potatoes, however, consist of car-load shipments together with the amount hauled by farmers directly to towns and cities. As no data are available on the latter point, a detailed study of the crop years 1920 to 1924 was made in an effort to discover what proportion of the potato crop on the average is trucked into cities directly by farmers. To do this, an estimate of the total urban consumption of potatoes in Minnesota had to be derived. The first step in approximating this amount was the reduction of the population figure to the equivalent adult male basis in order that the annual consumption of potatoes of the average adult male could be applied. The urban population of the state in 1920 was reduced to equivalent adult males by applying weights derived from those adopted by the United States Bureau of Labor Statistics.[15] As the census classification of the Minnesota population by age groups does not conform in all respects to the classification of ages used by the Bureau of Labor Statistics, the weights had to be adjusted to correspond with the census population.[16] As a result of this calculation, it was found that the urban population of the state in 1920 was equivalent to 882,738 adult males. The ratio of this number of adult males to the total urban population in 1920 was .8394, which was applied to the estimates of urban population for the years 1921, 1922, 1923, and 1924 in order to secure the approximate number of equivalent adult males in Minnesota in each of these years.

According to the cost-of-living survey of the United States Bureau of Labor Statistics in 1918-19, the average annual consumption of potatoes by the equivalent adult male in the north central states was 251.67 pounds or 4.19 bushels.[17] The estimated total urban consumption for Minnesota for each year from 1920 to 1924 was obtained by multiplying this amount by the estimated number of equivalent adult males for each year. This total consumption of potatoes was supplied not alone by amounts trucked in, but also by car-load shipments unloaded within the state, for which data are available. When the amount of car-lot unloads was subtracted from this estimated total consumption, the remainder represented the approximate amount trucked into cities and towns by the farmers. This amount was found to be close to 8 per cent of the total annual production in the years for which the detailed study was made, 1920-24. Consequently, for the years for which records of car-lot shipments are available (beginning with July, 1917), 8 per cent of the annual production has been added to the car-lot shipments to make up the total sales by the farmers. In all of the computations, car-lot shipments have been reduced to bushels on the basis of an average of 600 bushels to the car, which, according to marketing specialists, is considered the typical size of car by potato dealers.

A further observation of the data compiled for the years 1920-24 was that the car-lot shipments, as a whole, amounted to an average of 46.7 per cent of the total production. If 8 per cent of the total annual production is ordinarily hauled into towns and cities by the farmers themselves, then approximately an average of 55 per cent of the total annual crop is marketed. In years before car-lot shipments were recorded, 1910-1917, total sales of potatoes were, therefore, estimated by taking 55 per cent of the annual production reported by the United States Department of Agriculture.

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[15] United States Bureau of Labor Statistics, Bull. 357, p. 70. The weights are as follows: Adult male 1.00; adult female 0.90; child 11 to 14 years 0.90; child 7 to 10 years 0.75; child 4 to 6 years 0.40; child 3 years or under 0.15.

[16] For use in this study, adjustment of weights to conform with census age groups were made as follows: Adult male 1.00; adult female 0.90; child 10 to 14 years 0.85; child 5 to 9 years 0.61; child under 5 years 0.21.

[17] United States Bureau of Labor Statistics, Bull. 357, p. 113.

The total production of potatoes in the state and the total annual sales by farmers, estimated by the methods outlined, are shown in Table 34. These amounts apply to the crop year, as indicated.

Table 34

Production of Potatoes, and Amount Sold by the Farmers of Minnesota, 1910-1927
(Bushels)

Crop year (July to June)	Production*	Amount sold†
1910-11	13,420,000	7,381,000
1911-12	25,875,000	14,231,250
1912-13	33,075,000	18,191,250
1913-14	30,250,000	16,637,500
1914-15	30,780,000	16,929,000
1915-16	30,210,000	16,615,500
1916-17	16,800,000	9,240,000
1917-18	33,600,000	12,564,000
1918-19	32,760,000	16,726,000
1919-20	28,884,000	15,544,000
1920-21	31,581,000	16,848,000
1921-22	32,250,000	20,326,000
1922-23	43,740,000	20,849,000
1923-24	38,304,000	23,223,000
1924-25	44,880,000	22,606,000
1925-26	26,772,000	15,985,000
1926-27	29,800,000	17,273,112
1927-28	33,128,000	22,756,440

* U.S. Dept. of Agr. Yearbooks.

† For calendar year totals, see Table 36.

The monthly distribution of these annual crop year amounts from 1910 to 1916 have been based on an average of the percentages which the car-lot shipments of each month were of the total amount shipped in the crop year July to June, for the years 1917 to 1926. The percentage figures for each year and the average for the nine-year period are shown in Table 35. Since 1917 when car-lot shipments were first reported by months, the only percentage distribution required has been one to apply to the 8 per cent of production which is trucked into towns and cities. For this purpose, the nine-year average percentage has also been employed.

The actual amounts estimated as sold by the methods above outlined during each month of the period 1910-1927, together with calendar year totals, are shown in Table 36.

Prices of potatoes used in this study are the 15th of the month prices paid to producers, reported by the United States Department of Agriculture. These are shown in Table 37.

Table 35

Monthly Percentage Marketings of Minnesota Potatoes, Based on Amount Shipped in Car-Lots, for Year July to June, 1917-1926*

Month	1917	1918	1919	1920	1921	1922
January	...	7.7	7.8	8.5	6.4	6.4
February	...	9.2	5.8	5.3	7.4	4.9
March	...	12.9	10.0	8.6	10.6	15.0
April	...	8.1	6.9	4.7	4.8	8.5
May	...	3.8	4.3	1.2	3.6	3.7
June	...	1.0	1.8	0.5	0.9	0.8
July	...	0.4	0.4	0.3	...	1.8
August	8.0	13.2	11.0	6.0	3.5	5.0
September	11.7	19.5	24.3	12.1	17.0	14.4
October	24.7	19.7	26.4	29.7	30.0	24.4
November	8.8	7.4	6.0	14.3	7.3	8.5
December	4.1	3.2	3.1	3.9	2.9	2.3

Month	1923	1924	1925	1926	Average
January	6.0	7.6	9.8	6.8	7.4
February	5.3	11.5	12.1	10.6	8.0
March	14.6	11.4	13.2	11.8	12.0
April	11.3	7.2	6.1	7.2	7.2
May	4.8	3.0	4.3	3.5	3.6
June	1.6	0.9	1.1	1.2	1.1
July	...	0.1	2.2	...	0.6
August	5.2	1.8	11.5	...	7.2
September	18.3	8.4	15.5	...	15.7
October	23.5	27.7	20.3	...	25.2
November	8.1	11.6	6.3	...	8.7
December	3.3	3.8	3.1	...	3.3

* Computed from reports published in Crops and Markets.

Table 36

Amount of Potatoes Sold Monthly by the Farmers of Minnesota, 1910-1927 (Bushels)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	1,094,000	546,000	1,053,000	1,346,000	1,231,000	1,253,000	1,230,000	684,000	956,000
February	1,183,000	590,000	1,138,000	1,455,000	1,331,000	1,354,000	1,329,000	739,000	1,121,000
March	1,774,000	886,000	1,708,000	2,183,000	1,997,000	2,031,000	1,994,000	1,109,000	1,594,000
April	1,064,000	531,000	1,025,000	1,310,000	1,198,000	1,219,000	1,196,000	665,000	991,000
May	532,000	266,000	512,000	655,000	599,000	593,000	598,000	333,000	472,000
June	163,000	81,000	157,000	200,000	183,000	203,000	183,000	102,000	137,000
July	44,000	85,000	109,000	100,000	102,000	100,000	55,000	25,000	74,000
August	531,000	1,025,000	1,310,000	1,198,000	1,219,000	1,196,000	665,000	981,000	2,048,000
September	1,159,000	2,234,000	2,856,000	2,612,000	2,658,000	2,609,000	1,451,000	1,573,000	3,155,000
October	1,860,000	3,586,000	4,584,000	4,193,000	4,266,000	4,187,000	2,328,000	3,121,000	3,434,000
November	642,000	1,238,000	1,582,000	1,447,000	1,473,000	1,446,000	804,000	1,101,000	1,268,000
December	244,000	470,000	600,000	549,000	559,000	548,000	305,000	494,000	541,000
Total	10,290,000	11,538,000	16,634,000	17,248,000	16,816,000	16,739,000	12,138,000	10,927,000	15,791,000

Month	1919	1920	1921	1922	1923	1914	1925	1926	1927
January	1,297,000	1,296,000	1,099,000	1,327,000	1,293,000	1,768,000	2,124,000	1,100,000	1,242,616
February	1,025,000	882,000	1,266,000	1,071,000	1,199,000	2,556,000	2,584,000	1,638,000	1,932,520
March	1,734,000	1,417,000	1,822,000	2,976,000	2,949,000	2,661,000	2,937,000	1,884,000	2,525,880
April	1,156,000	782,000	864,000	1,694,000	2,217,000	1,672,000	1,426,000	1,152,000	1,459,248
May	705,000	240,000	600,000	741,000	960,000	717,000	946,000	570,000	834,024
June	289,000	95,000	160,000	177,000	327,000	208,000	252,000	187,000	131,824
July	64,000	54,000	15,000	330,000	27,000	39,000	312,000	14,000	29,101
August	1,629,000	1,038,000	815,000	1,111,000	1,274,000	601,000	1,743,000	752,000	912,617
September	3,578,000	2,136,000	3,421,000	3,049,000	4,175,000	2,159,000	2,488,000	1,891,000	3,256,488
October	4,072,000	4,894,000	5,964,000	5,119,000	5,514,000	6,176,000	3,350,000	4,574,000	6,117,660
November	995,000	2,274,000	1,524,000	1,784,000	1,894,000	2,515,000	1,054,000	1,319,000	2,153,571
December	492,000	642,000	600,000	510,000	758,000	846,000	507,000	597,000	753,458
Total	17,036,000	15,750,000	18,150,000	19,889,000	22,587,000	21,918,000	19,723,000	15,678,000	21,349,007

Table 37

Monthly Farm Prices for Potatoes Received by Producers in Minnesota,* 1910-1927

(Fifteenth of the month)
(Per bushel)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	$0.34	$0.56	$0.68	$0.30	$0.52	$0 32	$0.58	$1.50	$0.94
February	.34	0.58	0.78	.30	.54	.35	0.66	1.85	.84
March	.32	0.58	0.90	.28	.54	.37	0.71	2.05	.63
April	.26	0.62	1.04	.27	.52	.38	0.72	2.26	.50
May	.23	0.66	1.04	.28	.52	.40	0.70	2.46	.49
June	.24	0.80	0.90	.25	.59	.40	0.72	2.33	.58
July	.44	1.08	0.72	.36	.64	.46	0.73	1.85	.80
August	.80	1.05	0.50	.46	.56	.42	0.90	1.17	.94
September	.90	0.76	0.34	.45	.46	.30	1.00	0.88	.92
October	.76	0.57	0.28	.49	.37	.30	1.11	0.96	.82
November	.65	0.54	0.27	.50	.32	.36	1.28	0.98	.74
December	0.59	0.62	0.29	0.52	0.31	0.44	1.35	0.92	0.75

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	$0.78	$1.98	$0.74	$0.90	$0.34	$0.50	$0.37	$1.96	$1.14
February	0.72	2.30	0.62	.95	.34	0.49	0.40	1.90	1.10
March	0.69	2.73	0.56	.89	.36	0.55	0.40	1.90	1.00
April	0.80	3.46	0.50	.83	.42	0.56	0.38	2.20	1.00
May	0.84	3.84	0.38	.86	.43	0.56	0.39	1.90	1.20
June	0.80	3.44	0.38	.92	.44	0.70	0.46	1.50	1.65
July	1.33	2.65	1.06	.88	.70	0.93	0.94	1.80	1.80
August	1.72	1.89	1.60	.66	.80	1.04	1.12	1.40	1.40
September	1.50	1.21	1.28	.44	.60	0.57	0.87	1.10	0.85
October	1.50	0.83	1.00	.34	.43	0.35	0.99	1.00	0.65
November	1.53	0.77	0.92	.32	.44	0.32	1.80	1.25	0.60
December	1.62	0.79	0.86	0.34	0.48	0.34	1.82	1.10	0.60

* Prices 1910-25, U.S. Dept. of Agr. Statistical Bull. 15.
Prices 1926-27, current numbers of Crops and Markets.

Hogs

The actual numbers of hogs sold to packing plants and stockyards each month from Minnesota have been determined by the Division of Agricultural Statistics, Minnesota State Department of Agriculture, in co-operation with the Division of Crop and Livestock Estimates of the United States Bureau of Agricultural Economics, for the years 1920 to 1927, inclusive. These data represent the shipments received at central markets from Minnesota points, together with the number sold by farmers directly to local packers. Hogs sold to buyers at concentration points are also included. Duplication caused by reshipments is offset somewhat by the fact that sales by farmers to retail slaughter houses, local butchers and other similar buyers are not included.

For the years 1910 to 1919 the estimated number of hogs sold by the farmers of Minnesota has been based upon the average ratio which was found to exist, during the years from 1920 to 1926, between the receipts from Minnesota at South St. Paul and the total number of hogs sold from Minnesota during the same period, as reported by the Minnesota State Department of Agriculture. This ratio was then applied to the receipts from Minnesota at South St. Paul for each year from 1910 to 1919, to obtain the estimated number of hogs sold annually for the entire state. Because of the increasing tendency in recent years for packers to buy livestock outside of central markets, this method would tend to make the estimates high for the earlier years. The average ratio, therefore, was adjusted slightly to offset the inaccuracy.

The hundredweight of hogs sold has been found by applying the average weight of hogs marketed at South St. Paul in each month to the actual number of hogs marketed by the farmers of Minnesota in the corresponding month of the period from 1920 to 1927. For the earlier period, 1910-1919, the average annual weight of hogs marketed at South St. Paul was applied to the estimated annual number sold, to obtain the amount sold in hundredweight.

The number of hogs sold annually by the farmers of Minnesota, and the hundredweight estimate as above outlined for the years 1910-1927, are shown in Table 38.

Table 38

Estimated Number and Hundredweight of Hogs Sold by the Farmers of Minnesota, 1910-1927

Year	Number of hogs	Hundredweight
1910	1,111,598	2,501,096
1911	1,307,854	2,851,122
1912	1,408,112	3,168,252
1913	1,689,328	3,902,348
1914	1,800,032	3,978,071
1915	2,241,012	4,482,024
1916	2,745,722	5,381,615
1917	2,093,158	3,851,411
1918	2,457,649	5,062,757
1919	2,596,320	5,763,830
1920	2,637,261*	5,768,309
1921	2,914,511	6,194,782
1922	3,395,893	7,742,296
1923	4,405,793	9,506,368
1924	4,778,821	9,951,804
1925	4,372,370	9,395,234
1926	4,543,189	9,855,076
1927	4,684,401	10,173,278

* Minnesota Crop Reporter, March 1929. For the years 1920 to 1923, inclusive, final figures were used. For 1924 to 1927, preliminary figures were used which have undergone slight revision subsequently as published in the reference cited. Numbers for 1910-1919 estimated as explained in text.

A monthly percentage distribution is required only for the annual amounts of the years 1910 to 1919, and for this purpose the average percentage of hundredweight sold in each month of the period 1920-1926 has been used. This percentage distribution is shown in Table 39.

Table 39

Monthly Percentage Marketings of Minnesota Hogs, Based on Receipts (in Hundredweight) at Central Markets, 1920-1926

Month	1920	1921	1922	1923	1924	1925	1926	Average
January	12.6	11.8	10.7	11.7	12.9	12.9	11.3	11.9
February	10.1	11.2	8.2	9.3	10.0	10.3	8.5	9.7
March	9.5	8.1	7.2	9.3	9.3	8.0	10.0	8.8
April	6.8	6.7	6.1	6.8	8.4	8.1	7.3	7.2
May	9.7	7.8	8.9	8.1	7.4	6.9	7.3	8.0
June	9.4	7.8	11.1	8.1	7.7	7.1	7.3	8.3
July	6.0	5.6	6.7	6.8	7.8	5.7	8.1	6.7
August	4.0	5.5	5.3	4.7	4.3	3.8	5.2	4.7
September	4.0	4.6	4.4	4.6	3.6	4.7	4.8	4.4
October	7.7	8.3	7.6	8.2	5.8	8.3	6.5	7.5
November	9.7	11.2	10.8	10.4	8.5	10.3	9.5	10.1
December	10.6	11.3	13.0	11.9	14.3	13.8	14.2	12.7

The average percentage distribution was then applied to the annual sales in hundredweight for the years 1910-1919, and the monthly amounts which resulted, together with the data for the years 1920-1927, which were given originally by months, are shown in Table 40.

The prices of hogs used in this study are the monthly farm prices for the 15th of the month, reported by the United States Department of Agriculture. These are shown in Table 41.

Table 40

Hundredweight of Hogs Sold Monthly by the Farmers of Minnesota,* 1910-1927

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	297,630	339,284	377,022	464,379	473,390	533,361	640,412	458,318	602,468
February	242,606	276,559	307,320	378,528	385,873	434,756	522,017	373,587	491,087
March	220,096	250,899	278,806	343,407	350,070	394,418	473,582	338,924	445,523
April	180,078	205,281	228,114	280,969	286,421	322,706	387,476	277,302	364,519
May	200,088	228,090	253,460	312,188	318,246	358,562	430,529	308,113	405,021
June	207,591	236,643	262,965	323,895	330,180	372,008	446,674	319,667	420,209
July	167,573	191,025	212,273	261,457	266,531	300,296	360,568	258,045	339,205
August	117,552	134,003	148,908	183,410	186,969	210,655	252,936	181,016	237,950
September	110,048	125,449	139,403	171,703	175,035	197,209	236,791	169,462	222,761
October	187,582	213,834	237,619	292,676	298,355	336,152	403,621	288,856	379,707
November	252,611	287,963	319,993	394,137	401,785	452,684	543,543	388,993	511,338
December	317,639	362,092	402,368	495,598	505,215	569,217	683,465	489,129	642,970
Total	2,501,094	2,851,122	3,168,251	3,902,347	3,978,070	4,482,024	5,381,614	3,851,412	5,062,758

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	685,896	728,965	731,120	825,542	1,108,987	1,279,436	1,215,332	1,115,025	1,175,279
February	559,092	581,045	697,165	633,263	879,584	997,452	965,029	834,923	762,347
March	507,217	533,982	502,729	554,360	884,607	926,003	752,067	987,295	832,552
April	414,996	392,846	415,596	470,968	642,235	833,699	757,315	719,633	710,561
May	461,106	562,776	484,023	688,307	774,514	737,705	652,345	718,819	768,331
June	478,398	541,133	481,387	857,476	774,572	763,248	670,949	717,891	850,698
July	386,177	349,466	348,748	515,882	649,550	772,979	537,595	800,577	746,526
August	270,900	231,312	339,061	412,805	448,692	423,508	355,833	509,284	502,334
September	253,609	231,244	287,483	344,150	441,456	362,475	442,440	468,912	453,270
October	432,287	442,568	515,949	592,260	780,212	579,444	784,084	645,197	763,861
November	582,147	559,557	691,082	837,903	990,305	849,390	965,423	939,962	1,154,081
December	732,006	613,415	700,439	1,009,380	1,131,654	1,426,465	1,296,822	1,397,558	1,453,438
Total	5,763,831	5,768,309	6,194,782	7,742,296	9,506,368	9,951,804	9,395,234	9,855,076	10,173,278

* Calendar year totals which result from the addition of the 12 months frequently do not agree exactly with the yearly totals originally given, owing to slight deviations above or below 100 of the total percentage distribution for an individual year.

Table 41

Monthly Farm Prices for Hogs Received by Producers in Minnesota,* 1910-1927

(Fifteeenth of the month)
(Per hundredweight)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	$7.80	$ 7.30	$5.60	$6.80	$7.20	$6.40	$ 6.10	$ 9.30	$15.50
February	8.00	6.80	5.80	7.20	7.70	6.10	7.10	10.80	15.30
March	9.50	6.30	5.90	7.80	7.70	6.10	8.50	13.00	16.00
April	9.40	6.00	6.80	8.10	7.80	6.30	8.40	14.60	16.20
May	8.50	5.40	6.70	7.50	7.70	6.60	8.60	14.70	16.20
June	8.60	5.30	6.70	7.60	7.30	6.70	8.50	14.50	15.70
July	8.10	5.70	6.70	7.90	7.50	6.60	8.60	14.00	15.90
August	7.50	6.40	7.10	7.70	8.00	6.20	8.90	15.00	17.50
September	7.80	6.40	7.50	7.40	7.80	6.40	9.50	16.70	18.30
October	7.80	5.80	7.70	7.40	7.20	7.00	8.60	16.60	17.10
November	7.20	5.60	7.20	7.00	6.70	6.10	8.70	15.30	16.30
December	6.90	5.40	7.00	7.00	6.40	5.60	8.80	16.10	16.10

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	$16.20	$13.30	$8.40	$6.50	$7.60	$6.20	$ 9.00	$11.00	$10.90
February	16.00	13.40	8.30	8.60	7.40	6.10	9.30	11.70	11.00
March	17.00	13.60	9.00	9.30	7.30	6.30	12.20	11.70	10.90
April	18.70	13.60	7.70	9.10	7.30	6.30	11.90	11.30	10.30
May	19.10	13.60	7.60	9.40	6.90	6.40	10.80	11.80	9.30
June	18.70	13.10	6.80	9.30	6.00	6.20	10.90	12.80	7.90
July	20.10	13.30	7.70	8.90	6.10	6.20	12.00	12.30	8.10
August	19.70	13.40	8.50	8.10	6.50	8.60	12.20	11.10	8.60
September	15.50	13.90	6.50	7.70	7.50	8.30	11.40	11.60	9.40
October	13.50	13.00	6.00	8.00	6.60	9.10	11.00	11.70	10.00
November	13.10	11.60	5.90	7.40	6.10	8.40	10.40	11.20	8.60
December	12.60	9.00	6.00	7.40	5.70	8.00	10.40	10.80	7.80

* Prices 1910-25, U.S. Dept. of Agr. Statistical Bull. 15.
Prices 1926-27, current numbers of Crops and Markets.

Cattle and Calves

The numbers of cattle and calves sold monthly by Minnesota farmers have been furnished also by the Minnesota State Department of Agriculture, for the period 1920 to 1927. For the years 1911 to 1919, the marketings of each were estimated by applying to the receipts at South St. Paul from Minnesota the average ratio which existed for the period 1920 to 1926 between the total number marketed by Minnesota farmers and the receipts at South St. Paul from Minnesota. Receipts of cattle and calves were not reported separately in 1910. Separation was made by applying to the combined receipts of cattle and calves for 1910, the ratio which existed between receipts of cattle and calves for the period 1911 to 1919. Estimates of the hundredweight sold by months were made by the same methods as those used for hundredweight sales of hogs.

The number of cattle and calves sold by the farmers of Minnesota together with the estimated number of hundredweight are shown in Tables 42 and 43.

Table 42

Estimated Number and Hundredweight of Cattle Sold by the Farmers of Minnesota, 1910-1927

Year	Number of cattle	Hundredweight
1910	303,769	2,411,926
1911	369,744	2,909,885
1912	370,592	2,946,206
1913	344,592	2,729,168
1914	392,695	3,204,391
1915	622,738	5,025,496
1916	643,630	5,142,604
1917	706,372	5,318,981
1918	783,633	6,041,810
1919	651,502	4,970,960
1920	632,642*	5,156,194
1921	507,861	4,188,970
1922	625,962	5,194,497
1923	563,726	4,671,856
1924	567,336	4,904,910
1925	612,456	5,348,937
1926	735,562	6,416,757
1927	655,424	5,758,518

* Minnesota Crop Reporter, March 1929. For the years 1920 to 1925, inclusive, final figures for cattle and calves were used. For 1926 and 1927, preliminary figures were used which have undergone slight revision subsequently. Numbers for 1910-1919 estimated as explained in text.

Table 43

Estimated Number and Hundredweight of Calves Sold by the Farmers of Minnesota, 1910-1927

Year	Number of calves	Hundredweight
1910	135,212	221,748
1911	110,408	188,798
1912	117,478	209,111
1913	99,114	206,157
1914	105,904	241,461
1915	131,199	279,454
1916	164,468	314,134
1917	179,345	365,864
1918	223,590	427,057
1919	266,838	381,578
1920	336,343*	449,479
1921	316,047	432,495
1922	424,456	593,173
1923	453,465	621,510
1924	513,031	642,650
1925	619,925	777,700
1926	690,306	844,977
1927	638,502	798,545

* Minnesota Crop Reporter, March 1929. For the years 1920 to 1925, inclusive, final figures for cattle and calves were used. For 1926 and 1927, preliminary figures were used which have undergone slight revision subsequently. Numbers for 1910-1919 estimated as explained in text.

The percentage distributions used to derive monthly sales for cattle and calves separately for the period 1910-1919 were the averages of the monthly percentages of hundredweight of each sold during 1920-1926, shown in Tables 44 and 45. No percentage distributions were required after 1919, as the data were available by months.

These average monthly percentage distributions were applied to the annual number of hundredweight of cattle and calves estimated as sold in the years 1910 to 1919, to determine the monthly sales of each in these years. The amounts thus derived, hundredweight sales by months from 1920 to 1927, together with calendar year totals, are given in Tables 46 and 47 for cattle and calves, respectively.

The prices for cattle and calves are the 15th of the month prices, reported by the United States Department of Agriculture. These are shown for cattle in Table 48 and for calves in Table 49.

Table 44

Monthly Percentage Marketings of Minnesota Cattle, Based on Receipts (in Hundredweight) at Central Markets, 1920-1926

Month	1920	1921	1922	1923	1924	1925	1926	Average
January	9.6	10.2	7.6	10.5	9.0	9.4	8.5	9.3
February	9.2	7.1	7.7	7.7	8.1	8.5	7.3	7.9
March	10.9	11.2	9.6	8.4	8.9	10.7	9.2	9.8
April	7.3	7.7	7.9	8.0	9.5	9.7	8.0	8.3
May	7.0	8.0	8.5	7.2	8.0	7.9	8.3	7.8
June	5.0	6.8	6.5	5.9	6.0	5.8	8.2	6.3
July	4.9	3.6	7.3	6.5	7.2	5.1	7.6	6.0
August	8.2	8.5	9.2	7.6	5.3	5.0	5.2	7.0
September	10.7	7.3	8.3	9.1	6.7	7.1	7.1	8.0
October	10.3	11.7	10.0	11.2	9.8	10.3	10.1	10.5
November	10.8	10.9	9.4	8.5	10.4	9.3	11.1	10.1
December	5.9	6.9	8.0	9.3	11.2	11.2	9.4	8.9

Table 45

Monthly Percentage Marketings of Minnesota Calves, Based on Receipts (in Hundredweight) at Central Markets, 1920-1926

Month	1920	1921	1922	1923	1924	1925	1926	Average
January	7.6	8.4	7.2	9.2	8.6	7.4	8.1	8.1
February	8.9	8.8	7.4	7.2	8.3	7.8	8.4	8.1
March	12.2	12.1	9.6	8.0	8.6	9.8	9.4	10.1
April	10.4	8.2	8.6	9.3	10.0	10.7	8.8	9.4
May	9.5	10.0	10.1	13.9	10.6	9.8	9.2	10.4
June	11.7	11.3	9.9	9.5	8.3	8.4	8.8	9.7
July	7.1	6.2	8.5	7.3	8.2	6.3	6.8	7.2
August	6.4	6.4	7.6	6.8	5.3	5.0	5.5	6.1
September	5.5	5.8	6.1	5.6	6.3	7.1	6.4	6.1
October	6.5	7.4	9.0	8.5	8.8	8.8	9.0	8.3
November	7.8	8.7	8.7	7.9	7.3	8.4	10.0	8.4
December	6.3	6.6	7.3	6.8	9.8	10.6	9.5	8.1

Table 46

Hundredweight of Cattle Sold Monthly by the Farmers of Minnesota,* 1910-1927

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	224,309	270,619	273,997	253,813	298,008	467,371	478,262	494,665	561,888
February	190,542	229,881	232,750	215,604	253,147	397,014	406,266	420,199	477,303
March	236,369	285,169	288,728	267,458	314,030	492,499	503,975	521,260	592,097
April	200,190	241,520	244,535	226,521	265,964	417,116	426,836	441,475	501,470
May	188,130	226,971	229,804	212,875	249,942	391,989	401,123	414,881	471,261
June	151,951	183,323	185,611	171,938	201,877	316,606	323,984	335,096	380,634
July	144,716	174,593	176,772	163,750	192,263	301,530	308,556	319,139	362,509
August	168,835	203,692	206,234	191,042	224,307	351,785	359,982	372,329	422,927
September	192,954	232,791	235,696	218,333	256,351	402,040	411,408	425,518	483,345
Cctober	253,252	305,538	309,352	286,563	336,461	527,677	539,973	558,493	634,390
November	243,605	293,898	297,567	275,646	323,643	507,575	519,403	537,217	610,223
December	214,661	258,980	262,212	242,896	285,191	447,269	457,692	473,389	537,721
Total	2,409,514	2,906,975	2,943,258	2,726,439	3,201,184	5,020,471	5,137,460	5,313,661	6,035,768

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	462,299	496,274	427,507	392,421	490,580	439,175	503,296	542,230	637,123
February	392,706	476,198	296,040	399,784	357,402	397,920	454,932	468,961	525,176
March	487,154	560,621	469,638	496,448	395,100	435,511	570,284	590,195	533,604
April	412,590	377,797	324,597	409,360	374,329	467,573	519,028	512,904	441,825
May	387,735	361,163	335,449	442,506	340,737	390,195	422,558	530,169	423,738
June	313,170	258,145	284,442	338,657	276,858	293,806	309,987	524,302	403,145
July	298,258	253,892	152,430	380,167	304,464	355,124	273,858	490,122	360,997
August	347,967	424,400	357,903	478,117	355,609	259,902	269,913	332,165	390,715
September	397,677	551,830	306,456	432,525	426,182	327,924	378,832	457,761	435,957
October	521,951	533,316	489,846	520,899	521,522	479,709	549,843	651,814	577,249
November	502,067	557,134	454,304	490,467	398,655	509,976	499,846	710,728	601,817
December	442,415	305,424	290,358	413,146	430,418	548,095	596,560	605,386	427,172
Total	4,965,989	5,156,194	4,188,970	5,194,497	4,671,856	4,904,910	5,348,937	6,416,757	5,758,518

* Calendar year totals which result from the addition of the 12 months frequently do not agree exactly with the yearly totals originally given, owing to slight deviations above or below 100 of the total percentage distribution for an individual year.

Table 47

Hundredweight of Calves Sold Monthly by the Farmers of Minnesota,* 1910-1927

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	17,962	15,293	16,938	16,699	19,558	22,636	25,445	29,635	34,592
February	17,962	15,293	16,938	16,699	19,558	22,636	25,445	29,635	34,592
March	22,397	19,069	21,120	20,822	24,388	28,225	31,728	36,952	43,133
April	20,844	17,747	19,656	19,379	22,697	26,269	29,529	34,391	40,143
May	23,062	19,635	21,748	21,440	25,112	29,063	32,670	38,050	44,414
June	21,510	18,313	20,284	19,997	23,422	27,107	30,471	35,489	41,425
July	15,966	13,593	15,056	14,843	17,385	20,121	22,618	26,342	30,748
August	13,527	11,517	12,756	12,576	14,729	17,047	19,162	22,318	26,050
September	13,527	11,517	12,756	12,576	14,729	17,047	19,162	22,318	26,050
October	18,405	15,670	17,356	17,111	20,041	23,195	26,073	30,367	35,446
November	18,627	15,859	17,565	17,317	20,283	23,474	26,387	30,733	35,873
December	17,962	15,293	16,938	16,699	19,558	22,636	25,445	29,635	34,592
Total	221,751	188,799	209,111	206,158	241,460	279,456	314,135	365,865	427,058

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	30,908	34,287	36,426	42,948	57,249	55,193	57,674	68,540	74,885
February	30,908	39,953	38,204	43,648	44,834	53,211	61,037	71,311	79,976
March	38,539	54,686	52,345	56,845	49,752	55,105	75,890	79,800	79,654
April	35,868	46,921	35,476	51,120	57,996	64,354	83,069	74,569	70,210
May	39,684	42,856	43,241	60,182	86,424	67,878	76,227	77,866	74,092
June	37,013	52,749	48,803	58,474	58,816	53,206	65,284	73,941	63,510
July	27,474	31,889	27,018	50,611	45,564	53,060	48,691	57,287	51,757
August	23,276	28,924	27,672	45,048	42,087	34,043	38,574	46,183	46,002
September	23,276	24,774	24,937	36,295	34,600	40,196	55,010	54,459	51,069
October	31,671	28,936	32,208	53,452	52,561	56,318	68,292	75,792	69,308
November	32,053	35,188	37,734	51,373	49,078	47,125	65,624	84,815	75,356
December	30,908	28,316	28,431	43,177	42,549	62,961	82,328	80,414	62,726
Total	381,578	449,479	432,495	593,173	621,510	642,650	777,700	844,977	798,545

* Calendar year totals which result from the addition of the 12 months frequently do not agree exactly with the yearly totals originally given, owing to slight deviations above or below 100 of the total percentage distribution for an individual year.

Table 48

Monthly Farm Prices for Cattle Received by Producers in Minnesota,* 1910-1927

(Fifteenth of the month)
(Per hundredweight)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	$3.90	$3.70	$4.00	$5.00	$5.60	$5.30	$5.30	$6.10	$7.60
February	3.90	4.00	4.10	5.30	6.00	5.30	5.50	6.80	8.20
March	4.50	4.20	4.00	5.80	5.80	5.50	6.00	7.30	8.30
April	5.20	4.00	4.50	5.90	6.00	5.50	6.20	8.20	9.30
May	4.60	3.90	4.80	5.80	6.20	5.90	6.10	8.00	10.10
June	4.50	3.90	4.90	5.80	6.10	5.80	6.70	8.30	9.60
July	4.00	3.60	4.60	5.40	6.00	5.80	6.30	7.70	9.70
August	3.70	3.80	4.60	5.70	6.10	5.50	6.10	7.50	9.00
September	3.70	3.60	4.80	5.70	6.10	5.40	5.90	7.60	8.90
October	3.60	3.60	4.80	5.70	5.60	5.40	5.70	7.50	8.30
November	3.70	3.60	4.80	5.70	5.40	5.00	5.70	7.30	7.90
December	3.80	3.80	4.80	5.30	5.20	5.00	5.80	7.30	7.70

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	$ 9.00	$8.30	$5.40	$4.20	$4.70	$4.80	$5.20	$6.10	$6.30
February	9.10	8.10	5.20	5.00	5.10	4.80	5.30	6.40	6.50
March	9.90	8.20	6.00	5.00	5.20	5.10	6.00	6.40	6.90
April	10.20	8.40	5.30	5.00	5.30	5.40	6.20	6.60	7.20
May	10.30	8.40	5.50	5.10	5.50	5.60	6.70	6.70	7.20
June	9.80	8.50	4.90	5.50	5.50	5.50	6.40	6.60	7.40
July	9.60	7.90	4.80	5.10	5.40	5.40	6.40	6.60	6.90
August	9.20	7.50	4.80	4.90	5.20	5.70	6.30	6.20	7.20
September	8.10	7.30	4.60	4.80	5.40	5.60	6.10	6.50	6.70
October	7.50	7.40	4.10	4.70	4.90	5.30	6.40	6.10	7.30
November	7.50	5.70	3.90	4.40	4.40	5.40	5.90	5.70	7.60
December	7.70	5.00	4.10	4.50	4.60	4.60	5.80	6.00	8.00

* Prices 1910-25, U.S. Dept. of Agr. Statistical Bull. 15.
Prices 1926-27, current numbers of Crops and Markets.

Table 49

Monthly Farm Prices for Calves Received by Producers in Minnesota,* 1910-1927
(Fifteenth of the month)
(Per hundredweight)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	$5.80	$5.70	$5.90	$6.70	$7.80	$7.20	$7.20	$ 9.00	$11.00
February	5.70	5.70	6.00	6.90	7.60	7.20	7.80	10.00	10.70
March	6.40	5.80	5.70	7.30	7.30	7.10	8.10	9.60	10.80
April	5.70	5.20	5.70	7.40	7.50	7.00	7.90	10.50	11.30
May	6.00	5.10	5.70	7.20	7.40	7.00	7.90	10.30	11.30
June	5.60	5.00	6.00	7.50	7.40	7.30	8.20	10.60	11.60
July	5.70	5.00	6.00	7.70	7.40	7.40	8.50	11.00	12.10
August	5.80	5.10	6.20	7.10	7.90	7.20	8.70	10.50	12.20
September	5.40	5.40	6.00	7.40	7.90	7.40	8.70	11.10	12.80
October	5.70	5.30	6.70	7.40	7.60	7.60	8.40	11.10	12.60
November	5.40	5.40	6.10	7.80	7.40	7.10	8.40	10.10	11.60
December	5.80	5.30	6.60	7.50	7.20	7.10	8.60	10.90	12.00

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	$12.50	$13.30	$8.10	$6.40	$7.30	$7.60	$7.50	$ 9.40	$ 9.60
February	11.80	13.00	8.00	7.20	7.30	7.60	8.00	9.60	10.70
March	12.70	12.60	7.90	7.20	7.10	7.60	9.20	10.20	10.50
April	12.90	12.00	6.20	6.60	7.00	7.60	8.60	9.20	10.00
May	12.20	10.60	6.70	6.90	7.10	7.30	8.10	8.70	9.60
June	12.45	11.10	6.20	7.50	7.10	7.20	7.80	9.90	9.70
July	13.30	10.50	6.30	7.00	7.60	7.30	8.40	9.60	10.00
August	13.30	11.40	6.40	7.30	7.70	8.00	8.40	9.40	11.00
September	13.60	11.90	7.50	7.90	8.30	8.00	8.90	10.30	11.20
October	13.10	10.40	7.20	7.90	8.20	7.80	9.60	10.30	11.60
November	13.00	10.10	6.00	7.20	7.00	7.00	9.20	9.10	10.10
December	12.90	8.30	6.20	7.30	6.90	6.70	8.80	8.70	10.20

* Prices 1910-25, U.S. Dept. of Agr. Statistical Bull. 15.
Prices 1926-27, current numbers of Crops and Markets.

Lambs-Sheep

The combined numbers of lambs and sheep sold to packers each month from Minnesota have been compiled by the Minnesota State Department of Agriculture for the years 1920 to 1927. These figures are somewhat high for our use because of the inclusion of shipments from feeding stations, located at points in southwestern Minnesota. These institutions receive sheep from the range, fatten them, and reship to market. Feeding stations are not farms, and it is a mistake to include their product in farm receipts, but it seems impossible to make any separation. At present the business is not large and does not greatly detract from the accuracy of the data. The records of these data are for lambs and sheep combined, and no effort has been made to separate the numbers of each. The average weight per head, as reported for South St. Paul, did not distinguish between lambs and sheep, so that there seemed to be no objection to the application of these weights to the numbers of animals reported. The methods followed in estimating the number of lambs and sheep sold from 1910 to 1919, the number of hundredweight represented by these animals, the percentage distribution by months during 1910-1919, and the number of hundredweight sold during each month from 1910 to 1927, were in all essential respects the same as those outlined for hogs. These data are shown in Tables 50, 51, and 52.

Table 50

Estimated Number and Hundredweight of Lambs-Sheep Sold by the Farmers of Minnesota, 1910-1927

Year	Number of lamb-sheep	Hundredweight
1910	196,765	161,347
1911	200,573	168,481
1912	222,620	189,227
1913	170,481	139,794
1914	208,187	176,959
1915	168,462	136,454
1916	139,922	117,534
1917	115,063	97,804
1918	177,355	148,978
1919	310,994	239,465
1920	308,775*	232,718
1921	315,599	242,461
1922	294,845	220,325
1923	219,737	173,682
1924	261,932	210,966
1925	281,011	227,567
1926	379,167	337,676
1927	406,315	363,294

* Minnesota Crop Reporter, March, 1929. For the years 1920 to 1925, inclusive, final figures were used. For 1926 and 1927, preliminary figures were used which have undergone slight revision subsequently as published in the reference cited. Numbers for 1910-1919 estimated as explained in text.

Table 51

Monthly Percentage Marketings of Minnesota Lambs-Sheep, Based on Receipts (in Hundredweight) at Central Markets, 1920-1926

Month	1920	1921	1922	1923	1924	1925	1926	Average
January	15.2	10.7	12.9	9.5	8.3	7.0	6.7	10.0
February	8.9	6.8	6.5	4.8	4.2	3.4	4.2	5.5
March	1.8	4.5	3.1	1.9	2.1	2.0	2.5	2.7
April	1.7	1.8	1.0	0.8	1.4	1.7	1.1	1.4
May	1.4	2.2	1.4	0.9	1.0	1.0	0.5	1.2
June	1.6	2.9	2.3	1.6	1.4	1.1	1.7	1.8
July	3.5	3.2	5.8	4.4	3.5	3.8	3.2	3.9
August	7.5	12.1	14.6	9.8	9.0	10.4	7.7	10.2
September	13.9	13.6	18.7	20.0	16.7	19.0	16.5	16.9
October	17.3	19.9	14.7	21.6	23.1	21.6	22.0	20.0
November	18.4	13.9	11.8	14.8	16.4	17.5	17.9	15.8
December	8.8	8.3	7.1	10.1	12.9	11.5	15.9	10.6

Table 52

Hundredweight of Lambs-Sheep Sold Monthly by the Farmers of Minnesota,* 1910-1927

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	16,135	16,848	18,923	13,979	17,696	13,645	11,753	9,780	14,898
February	8,874	9,266	10,407	7,689	9,733	7,505	6,464	5,379	8,194
March	4,356	4,549	5,109	3,774	4,778	3,684	3,173	2,641	4,022
April	2,259	2,359	2,649	1,957	2,477	1,910	1,645	1,369	2,086
May	1,936	2,022	2,271	1,678	2,124	1,637	1,410	1,174	1,788
June	2,904	3,033	3,406	2,516	3,185	2,456	2,116	1,760	2,682
July	6,293	6,571	7,380	5,452	6,901	5,322	4,584	3,814	5,810
August	16,457	17,185	19,301	14,259	18,050	13,918	11,988	9,976	15,196
September	27,268	28,473	31,979	23,625	29,906	23,061	19,863	16,529	25,177
October	32,269	33,696	37,845	27,959	35,392	27,291	23,507	19,561	29,796
November	25,493	26,620	29,898	22,087	27,960	21,560	18,570	15,453	23,539
December	17,103	17,859	20,058	14,818	18,758	14,464	12,459	10,367	15,792
Total	161,347	168,481	189,226	139,793	176,960	136,453	117,532	97,803	148,980

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	23,947	35,311	26,034	28,513	16,436	17,538	15,867	22,761	31,038
February	13,171	20,792	16,555	14,287	8,326	8,787	7,654	14,094	23,111
March	6,466	4,084	10,866	6,762	3,252	4,434	4,638	8,431	12,759
April	3,353	3,975	4,452	2,311	1,398	2,955	3,909	3,866	4,187
May	2,874	3,289	5,341	3,015	1,601	2,018	2,232	1,552	2,324
June	4,310	3,856	7,105	5,084	2,808	2,913	2,522	5,814	5,611
July	9,339	8,075	7,811	12,783	7,624	7,469	8,614	10,927	10,904
August	24,425	17,458	29,302	32,268	16,937	19,052	23,759	25,921	36,499
September	40,470	32,359	32,951	41,194	34,612	35,306	43,201	55,828	61,140
October	47,893	40,311	48,300	32,340	37,454	48,661	49,158	74,226	93,253
November	37,835	42,745	33,720	26,076	25,671	34,598	39,781	60,405	57,265
December	25,383	20,463	20,024	15,692	17,563	27,235	26,232	53,851	25,203
Total	239,466	232,718	242,461	220,325	173,682	210,966	227,567	337,676	363,294

* Calendar year totals which result from the addition of the 12 months frequently do not agree exactly with the yearly totals originally given, owing to slight deviations above or below 100 of the total percentage distribution for an individual year.

The United States Department of Agriculture reports the prices paid to producers in Minnesota on the 15th of the month separately for lambs and sheep. The opinion of market specialists is that lambs and sheep are sold in Minnesota in the ratio of approximately 9 lambs to 1 sheep. In accordance with this, a composite price has been constructed for "lambs-sheep," in which the lamb price reported by the United States Department of Agriculture has been given a weighting of 9, and the sheep price a weighting of 1. The resulting composite price is shown in Table 53.

Table 53

Monthly Composite Price for Lambs-Sheep Received by Producers in Minnesota,* 1910-1927

(Fifteenth of the month)
(Per hundredweight)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	$6.05	$ 4.97	$4.86	$ 5.84	$ 5.74	$ 5.84	$ 6.82	$ 9.64	$12.74
February	6.05	4.87	5.06	5.84	5.87	6.04	7.11	10.32	12.61
March	7.01	4.50	5.06	6.16	5.56	6.34	7.81	10.66	13.26
April	7.14	4.90	5.39	6.17	5.87	6.47	7.91	11.81	14.23
May	6.37	4.59	6.04	5.78	5.95	6.74	7.84	11.55	14.30
June	6.45	4.86	5.74	5.98	6.23	6.98	8.18	11.60	14.19
July	5.56	5.24	5.54	6.06	6.31	6.70	7.99	11.99	14.11
August	4.89	4.93	5.53	5.65	6.34	6.33	7.89	11.42	13.67
September	5.08	4.50	4.98	5.81	5.94	6.23	7.98	13.05	14.10
October	5.16	4.59	5.07	5.63	5.83	6.34	7.68	13.40	12.67
November	4.98	4.49	5.16	5.65	5.74	6.42	7.89	12.80	12.43
December	5.07	4.29	5.53	5.63	5.93	6.24	8.58	13.02	12.28

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	$12.39	$12.81	$7.45	$ 7.33	$10.50	$ 9.94	$12.87	$12.60	$10.47
February	12.43	13.60	7.18	9.13	10.25	10.45	12.67	11.81	11.04
March	13.95	13.50	7.22	9.94	10.51	10.46	12.88	11.35	11.35
April	14.16	13.88	6.74	10.50	12.61	10.67	11.97	11.48	12.29
May	13.36	13.68	7.30	10.01	10.64	10.78	11.42	12.14	12.18
June	13.03	12.01	6.70	9.60	10.69	10.10	11.30	11.86	12.36
July	12.98	11.02	7.17	9.16	10.70	9.80	11.80	12.01	11.16
August	12.32	10.69	6.43	8.94	9.58	10.16	11.67	11.16	11.10
September	11.36	9.93	5.92	8.98	9.76	9.92	11.34	11.23	10.97
October	11.03	10.64	5.61	9.58	9.36	9.76	11.68	11.43	10.98
November	11.30	8.20	5.70	9.94	9.51	9.86	11.76	10.94	11.29
December	11.68	7.74	6.69	10.58	9.39	11.02	12.82	10.77	10.94

* Prices 1910-25, U.S. Dept. of Agr. Statistical Bull. No. 15.
Prices 1926-27, current numbers of Crops and Markets.
Composite price computed by a weighting of 9 to lamb prices, and 1 to sheep prices.

Chickens

Records of the pounds of chickens received monthly from Minnesota at the Boston, Chicago, New York, and Philadelphia markets, are available from 1922 to 1926. In addition to these amounts, the urban consumption for the state has been estimated on the basis of the number of equivalent adult males in the state during these years. The method by which the number of equivalent adult males was derived has been explained in other sections. Urban consumption of chickens was taken at 6.85 pounds per adult male, which is the average annual consumption reported by the United States Bureau of Labor Statistics as a result of the cost-of-living survey of 1918-19 in the north central states.[18] This amount of local consumption added to the receipts from Minnesota at the four eastern markets, constituted the estimated sales of the farmers of Minnesota for each of the years 1922 to 1927. For the period 1922-1926, the average ratio was computed between the amount estimated as sold annually and the number of chickens on farms. This number is reported by the Bureau of the Census for 1910, 1920, and 1925, and an estimate by straight-line interpolation was made for other years. This average ratio was then applied to the number of chickens on farms in each year from 1910 to 1922 in order to determine the approximate amount of sales by the farmers of Minnesota in these years. The number of chickens on farms and the amount of estimated sales are shown in Table 54.

Table 54
Number of Chickens on Farms and Pounds Estimated Sold Annually by the Farmers of Minnesota, 1910-1927

Year	Number of chickens	Pounds sold
1910	10,293,849*	22,111,187
1911	10,585,726	22,738,139
1912	10,877,603	23,365,091
1913	11,169,480	23,992,043
1914	11,461,357	24,618,994
1915	11,753,234	25,245,946
1916	12,045,111	25,872,898
1917	12,336,988	26,499,850
1918	12,628,865	27,126,802
1919	12,920,742	27,753,754
1920	13,212,619*	28,380,705
1921	13,851,711	29,753,475
1922	14,490,803	31,126,244
1923	15,129,895	28,211,686
1924	15,768,987	33,267,766
1925	16,408,080*	32,962,817
1926	17,047,173	40,053,549
1927	17,686,265	38,571,726

* U. S. Census of Agriculture, 1910, 1920, 1925.

The monthly marketings, beginning with 1922, were determined on the basis of the percentage which the receipts of each month from Minnesota at the four eastern markets constituted of the yearly state total. The average of these monthly percentages from 1922-26 was taken as the basis for distribution for the years 1910-1921. These percentage distributions are shown in Table 55.

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[18] United States Bureau of Labor Statistics. Bull. 357, p. 112.

Table 55

Monthly Percentage Marketings of Chickens Based on Receipts from Minnesota at Four Eastern Markets,* 1922-1926

Month	1922	1923	1924	1925	1926	Average
January	6.7	13.7	10.8	9.9	7.9	9.8
February	3.5	7.8	7.3	5.6	4.9	5.8
March	3.2	3.2	4.4	2.5	4.2	3.5
April	2.2	2.2	2.2	1.8	2.4	2.2
May	2.2	1.7	1.1	1.2	1.9	1.6
June	4.1	1.5	2.7	3.2	3.9	3.1
July	2.5	2.8	4.1	4.7	4.4	3.7
August	2.8	2.7	3.3	5.1	5.1	3.8
September	3.2	3.4	4.7	5.2	6.3	4.6
October	5.0	7.5	8.3	8.7	8.6	7.6
November	21.4	19.5	20.6	21.4	23.5	21.3
December	43.1	33.9	30.5	30.7	26.8	33.0

* New York, Boston, Philadelphia, and Chicago.

Table 56 shows the amounts of estimated sales by months, on the basis of this distribution.

The prices for chickens are for the 15th of the month, reported by the United States Department of Agriculture. These are shown in Table 57.

Table 56

Amounts of Chickens Sold Monthly by the Farmers of Minnesota,* 1910-1927 (Pounds)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	2,166,896	2,228,338	2,289,779	2,351,220	2,412,661	2,474,103	2,535,544	2,596,985	2,658,427
February	1,282,449	1,318,812	1,355,175	1,391,538	1,427,902	1,464,265	1,500,628	1,536,991	1,573,355
March	773,892	795,835	817,778	839,721	861,665	883,608	905,551	927,495	949,438
April	486,446	500,239	514,032	527,825	541,618	555,411	569,204	582,997	596,790
May	353,779	363,810	373,841	383,873	393,904	403,935	413,966	423,998	434,029
June	685,447	704,882	724,318	743,753	763,189	782,624	802,060	821,495	840,930
July	818,114	841,311	864,508	887,706	910,903	934,100	957,297	980,494	1,003,692
August	840,225	864,049	887,873	911,698	935,522	959,346	983,170	1,006,994	1,030,818
September	1,017,115	1,045,954	1,074,794	1,103,634	1,132,474	1,161,314	1,190,153	1,218,993	1,247,833
October	1,680,450	1,728,099	1,775,747	1,823,395	1,871,043	1,918,692	1,966,340	2,013,989	2,061,637
November	4,709,683	4,843,224	4,976,764	5,110,305	5,243,846	5,377,386	5,510,927	5,644,468	5,778,009
December	7,296,692	7,503,586	7,710,480	7,917,374	8,124,268	8,331,162	8,538,056	8,744,951	8,951,845
Total	22,111,188	22,738,139	23,365,089	23,992,042	24,618,995	25,245,946	25,872,896	26,499,850	27,126,803

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	2,719,868	2,781,309	2,915,841	2,085,458	3,865,001	3,592,919	3,263,319	3,164,230	3,352,388
February	1,609,718	1,646,081	1,725,702	1,089,419	2,200,511	2,428,547	1,845,918	1,962,624	1,733,994
March	971,381	993,325	1,041,372	996,040	902,774	1,463,782	824,070	1,682,249	1,194,529
April	610,583	624,375	654,576	684,777	620,657	731,891	593,331	961,285	655,064
May	444,060	454,091	476,056	684,777	479,599	365,945	395,554	761,017	924,797
June	860,366	879,802	922,358	1,276,176	423,175	898,230	1,054,810	1,562,088	1,194,529
July	1,026,889	1,050,086	1,100,879	778,156	789,927	1,363,978	1,549,252	1,762,356	1,040,396
August	1,054,643	1,078,467	1,130,632	871,535	761,716	1,097,836	1,681,104	2,042,731	1,618,394
September	1,276,673	1,305,512	1,368,660	996,040	959,197	1,563,585	1,714,066	2,523,374	2,389,058
October	2,109,285	2,156,934	2,261,264	1,556,312	2,115,876	2,761,225	2,867,765	3,444,605	4,161,585
November	5,911,550	6,045,090	6,337,490	6,661,016	5,501,279	6,853,160	7,054,043	9,412,584	9,710,364
December	9,158,739	9,365,633	9,818,647	13,415,411	9,563,762	10,146,669	10,119,585	10,734,351	10,596,628
Total	27,753,755	28,380,705	29,753,477	31,095,117	28,183,474	33,267,767	32,962,817	40,013,494	38,571,726

* Calendar year totals which result from the addition of the 12 months frequently do not agree exactly with the yearly totals originally given, owing to slight deviations above or below 100 of the total percentage distribution for an individual year.

Table 57

Monthly Farm Prices for Chickens Received by Producers in Minnesota,* 1910-1927

(Fifteenth of the month)
(Per pound)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	$0.093	$0.091	$0.085	$0.088	$0.102	$0.091	$0.097	$0.127	$0.155
February	.094	.090	.088	.094	.100	.095	.102	.130	.170
March	.098	.091	.093	.100	.105	.099	.108	.140	.175
April	.100	.095	.096	.102	.112	.104	.123	.152	.185
May	.100	.094	.096	.102	.114	.108	.118	.157	.185
June	.101	.090	.096	.102	.109	.099	.117	.150	.184
July	.102	.094	.094	.114	.107	.101	.120	.150	.195
August	.104	.098	.096	.114	.112	.100	.116	.150	.200
September	.100	.094	.098	.114	.106	.104	.123	.167	.208
October	.094	.088	.096	.103	.106	.098	.125	.154	.198
November	.090	.082	.093	.098	.091	.092	.124	.130	.173
December	0.090	0.082	0.088	0.096	0.089	0.088	0.120	0.143	0.172

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	$0.184	$0.192	$0.200	$0.160	$0.140	$0.135	$0.158	$0.184	$0.177
February	.183	.216	.200	.170	.140	.147	.170	.189	.175
March	.195	.235	.200	.170	.150	.158	.174	.186	.176
April	.210	.240	.210	.180	.159	.159	.180	.202	.184
May	.230	.248	.190	.180	.157	.174	.183	.200	.175
June	.210	.220	.150	.170	.160	.157	.180	.194	.151
July	.210	.215	.170	.170	.150	.170	.177	.192	.156
August	.220	.232	.190	.160	.160	.178	.180	.185	.163
September	.210	.240	.170	.160	.160	.183	.172	.181	.162
October	.180	.200	.150	.160	.150	.164	.163	.171	.158
November	.160	.210	.140	.130	.136	.156	.150	.165	.159
December	0.180	0.200	0.150	0.130	0.127	0.151	0.162	0.171	0.169

* Prices 1910-25, U. S. Dept. of Agr. Statistical Bull. 15.
Prices 1926-27, current numbers of Crops and Markets.

Eggs

Estimates of total egg production depend primarily upon census data. The census reports production for 1919 and 1924, and production for intercensus years has been estimated by straight-line interpolation. The average ratio between these estimated amounts of annual production and the number of chickens on farms was computed for the period 1919-1924 and applied to the number of chickens on farms for each year from 1910 to 1918, and for 1925, 1926, and 1927. The results were accepted as the production for each year in the period.

Annual sales of eggs were estimated at 65 per cent of total production, which was the most accurate estimate obtainable. This method of estimating production and sales is admittedly faulty. It is substantiated reasonably well, however, for the period 1922 to 1925 by the receipts of eggs from Minnesota at the four principal eastern markets,[19] plus an amount to cover urban consumption within the state estimated at the rate of 15.86 dozens per equivalent adult male, which is the amount reported by the United States Bureau of Labor Statistics in its 1918-19 cost-of-living survey in the north central states.[20] Estimates of sales made in this manner average about 1,000,000 dozen per year less than the estimates made by taking a flat percentage of total production. It is believed that the figure for urban consumption is low, because the equivalent adult male consumption estimate is derived from budgets of working people for whom eggs are more or less a luxury, particularly in the winter months. Neither does this method include the consumption of eggs in towns smaller than 2,500 population, nor receipts of eggs at other than the four principal markets. There must be appreciable amounts shipped from Minnesota to other cities. If such allowances as these could be incorporated, it seems likely that the estimates which have been made would be substantially verified. The figures presented in this section, however, should be considered as rough approximations only. The amounts sold by the farmers of Minnesota, estimated as above outlined, are shown in Table 58.

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[19] New York, Boston, Philadelphia, and Chicago.

Table 58

Estimated Amount of Eggs Sold by Farmers of Minnesota, 1910-1927
(Dozens)

Year	Amount	Year	Amount
1910	29,099,166	1919	37,639,899
1911	30,165,084	1920	40,355,962
1912	31,244,283	1921	42,623,099
1913	32,336,762	1922	44,919,316
1914	33,442,520	1923	47,244,610
1915	34,561,559	1924	49,609,020
1916	35,693,880	1925	51,982,438
1917	36,839,479	1926	54,394,972
1918	37,998,360	1927	56,836,581

The percentage distribution on which to base monthly marketings of eggs has also received considerable attention. The percentage which the monthly receipts from Minnesota at the Chicago, New York, Boston, and Philadelphia markets constituted of the annual receipts is available from 1922 to 1926. These figures, together with the average percentage for the five-year period, are shown in Table 59.

[20] United States Bureau of Labor Statistics, Bull. 357, p. 112.

Table 59

Monthly Percentage Marketings of Eggs Based on Receipts from Minnesota at Four Eastern Markets,* 1922-1926, and Receipts of Selected Co-operative Associations in Minnesota, 1925

	Percentages based on						
	Receipts of four eastern markets from Minnesota						Receipts of co-operative associations, 1925
Month	1922	1923	1924	1925	1926	Average	
January	2.1	2.0	3.1	1.4	3.5	2.4	2.6
February	2.2	1.9	3.8	3.5	3.5	3.0	5.6
March	3.5	5.4	9.5	8.5	7.7	6.9	13.8
April	15.1	11.8	16.6	17.1	16.7	15.5	19.3
May	23.5	20.2	18.6	16.2	17.9	19.3	15.7
June	17.8	18.3	13.6	15.4	17.2	16.5	13.6
July	11.2	11.4	11.4	10.7	10.0	10.9	10.1
August	9.6	9.3	7.8	9.5	8.9	9.0	8.7
September	8.2	8.4	7.3	8.5	7.7	8.0	6.0
October	4.0	6.2	4.8	4.4	3.6	4.6	2.0
November	1.8	3.0	2.0	2.4	1.6	2.2	0.7
December	1.0	2.1	1.5	2.4	1.7	1.7	1.9

* New York, Boston, Philadelphia, and Chicago.

Additional information for 1925, on the monthly marketings of the farmers who delivered eggs to co-operative associations, was also available. The receipts of nine of the associations which had functioned during the entire 12 months of 1925, resulted in the distribution shown in the last column of Table 59. This distribution confirmed the opinion of those who have followed egg-marketings that in recent years there has been more and more of a tendency for the peak of marketings in the early spring and summer months to flatten out and for marketings in February and especially in March to be larger than formerly. From the information at hand, it was decided to estimate the amounts sold each month by applying the percentage distribution of the last column in Table 59 to the estimated annual sales of eggs for the years 1924, 1925, 1926, 1927, and for the years before 1924, the average percentage of receipts at the four eastern markets.

When the percentage distributions were applied to the estimated annual sales of eggs, monthly sales of the amounts shown in Table 60 resulted.

The prices for eggs used in this study are those reported for the 15th of the month by the United States Department of Agriculture, as shown in Table 61.

Table 60

Amount of Eggs Sold Monthly by the Farmers of Minnesota,* 1910-1927 (Dozens)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	698,380	723,962	749,863	776,082	802,620	829,477	856,653	884,147	911,961
February	872,975	904,953	937,328	970,103	1,003,276	1,036,847	1,070,816	1,105,184	1,139,951
March	2,007,842	2,081,391	2,155,856	2,231,237	2,307,534	2,384,748	2,462,878	2,541,924	2,621,887
April	4,510,371	4,675,588	4,842,864	5,012,198	5,183,591	5,357,042	5,532,551	5,710,119	5,889,746
May	5,616,139	5,821,861	6,030,147	6,240,995	6,454,406	6,670,381	6,888,919	7,110,019	7,333,684
June	4,801,362	4,977,239	5,155,307	5,335,566	5,518,016	5,702,657	5,889,490	6,078,514	6,269,729
July	3,171,809	3,287,994	3,405,627	3,524,707	3,645,235	3,767,210	3,890,633	4,015,503	4,141,821
August	2,618,925	2,714,858	2,811,985	2,910,309	3,009,827	3,110,540	3,212,449	3,315,553	3,419,852
September	2,327,933	2,413,207	2,499,543	2,586,941	2,675,402	2,764,925	2,855,510	2,947,158	3,039,869
October	1,338,562	1,387,594	1,437,237	1,487,491	1,538,356	1,589,832	1,641,918	1,694,616	1,747,925
November	640,182	663,632	687,374	711,409	735,735	760,354	785,265	810,469	835,964
December	494,686	512,806	531,153	549,725	568,523	587,547	606,796	626,271	645,972
Total	29,099,166	30,165,085	31,244,284	32,336,763	33,442,521	34,561,560	35,693,878	36,839,477	37,998,361

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	903,358	968,543	1,022,954	1,078,064	1,133,871	1,289,835	1,351,543	1,414,269	1,477,751
February	1,129,197	1,210,679	1,278,693	1,347,579	1,417,338	2,778,105	2,911,017	3,046,118	3,182,849
March	2,597,153	2,784,561	2,940,994	3,099,433	3,259,878	6,846,045	7,173,576	7,506,506	7,843,448
April	5,834,184	6,255,174	6,606,580	6,962,494	7,322,915	9,574,541	10,032,611	10,498,230	10,969,460
May	7,264,501	7,788,701	8,226,258	8,669,428	9,118,210	7,788,616	8,161,243	8,540,011	8,923,343
June	6,210,583	6,658,734	7,032,811	7,411,687	7,795,361	6,746,827	7,069,612	7,397,716	7,729,775
July	4,102,749	4,398,800	4,645,918	4,896,205	5,149,662	5,010,511	5,250,226	5,493,892	5,740,495
August	3,387,591	3,632,037	3,836,079	4,042,738	4,252,015	4,315,985	4,522,472	4,732,363	4,944,782
September	3,011,192	3,228,477	3,409,848	3,593,545	3,779,569	2,976,541	3,118,946	3,263,698	3,410,195
October	1,731,435	1,856,374	1,960,663	2,066,289	2,173,252	992,180	1,039,649	1,087,899	1,136,732
November	828,078	887,831	937,708	988,225	1,039,381	347,263	363,877	380,765	397,856
December	639,878	686,051	724,593	763,628	803,158	942,571	987,666	1,033,504	1,079,895
Total	37,639,899	40,355,962	42,623,099	44,919,315	47,244,610	49,609,020	51,982,438	54,394,971	56,836,581

* Calendar year totals which result from the addition of the 12 months frequently do not agree exactly with the yearly totals originally given, owing to slight deviations above or below 100 of the total percentage distribution for an individual year.

Table 61

Monthly Farm Prices for Eggs Received by Producers in Minnesota,* 1910-1927

(Fifteenth of the month)
(Per Dozen)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	$0.29	$0.26	$0.30	$0.24	$0.28	$0.31	$0.29	$0.35	$0.44
February	.25	.20	.28	.21	.26	.26	.28	.35	.44
March	.20	.15	.22	.18	.21	.18	.18	.27	.31
April	.18	.14	.16	.16	.16	.16	.18	.29	.30
May	.18	.14	.16	.16	.14	.16	.18	.30	.30
June	.17	.13	.16	.16	.16	.15	.18	.30	.31
July	.16	.13	.16	.16	.17	.16	.19	.29	.32
August	.16	.15	.17	.17	.19	.17	.21	.30	.34
September	.18	.17	.19	.20	.21	.18	.23	.34	.36
October	.22	.20	.22	.23	.23	.22	.29	.35	.41
November	.25	.24	.26	.29	.26	.27	.33	.37	.46
December	0.28	0.28	0.26	0.30	0.30	0.31	0.37	0.41	0.56

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	$0.52	$0.57	$0.51	$0.27	$0.36	$0.30	$0.44	$0.32	$0.34
February	.32	.48	.28	.38	.31	.30	.33	.26	.28
March	.32	.40	.26	.21	.25	.18	.20	.23	.21
April	.36	.36	.21	.21	.21	.17	.24	.25	.20
May	.39	.37	.17	.20	.21	.19	.24	.24	.19
June	.34	.34	.18	.20	.19	.20	.26	.25	.16
July	.35	.34	.24	.19	.18	.21	.27	.24	.19
August	.37	.41	.25	.18	.21	.24	.29	.24	.21
September	.39	.45	.27	.24	.26	.30	.26	.30	.25
October	.48	.50	.38	.31	.30	.36	.34	.35	.31
November	.57	.58	.45	.38	.38	.41	.42	.41	.36
December	0.68	0.65	0.49	0.45	0.40	0.46	0.42	0.44	0.41

* Prices 1910-25, U. S. Dept. of Agr. Statistical Bull. 15.
Prices 1926-27, current numbers of Crops and Markets.

Butterfat

Estimates of the quantity of butterfat sold were derived from the annual reports of the Minnesota State Department of Agriculture, Dairy and Food. For the most part, the pounds of butterfat received annually by the creameries of the state were available. For 1926, the estimate of the amount of butterfat sold by farmers had to be made before the figures of the Dairy and Food department were compiled, and the increase in receipts of the Land O'Lakes Creameries, Incorporated, in 1926 over their receipts in 1925 was taken as representative of butterfat sales in general and applied to the 1925 figure for the state in order to determine the total estimate for 1926. Such an estimate was essential if 1926 was to be included in the base period. A subsequent check on this procedure showed a difference of only about 2 per cent in the figure thus secured and the one which would have been computed later from the records of the Dairy and Food department. In 1927, the estimate of butterfat was derived from the total pounds of butter manufactured by Minnesota creameries as reported by the Dairy and Food department. From these annual amounts of butterfat received by Minnesota creameries, the amount estimated to have been resold to farmers, has been deducted. This item varies from 5.04 per cent of creamery receipts of butterfat in 1910 to 5.65 per cent in 1927.[21] The deduction was made because this amount did not represent a real sale but merely a trade of butterfat for butter, and consequently was not a factor in cash income. Cream retained at home for the production of butter would not be considered, and, from the standpoint of cash income, this "resale" of butter seemed more closely related to the home production of butter than to a sale-and-purchase transaction. The amount remaining after this deduction represented the approximate sales of Minnesota farmers. The method is faulty in assuming that the butter and butterfat reported by Minnesota creameries constituted sales of Minnesota farmers only. No data are available to show how much may have been shipped to Minnesota creameries from farmers outside the state, or how much the farmers of Minnesota may have shipped to creameries outside the state. The

Table 62

Receipts of Butterfat by Minnesota Creameries, Amount Resold to Farmers, and Amount of Actual Sales by the Farmers of Minnesota, 1910-1927

(Pounds)

Year	Receipts by Minnesota creameries*	Amount resold to farmers	Amount of actual sales
1910	80,637,000	4,066,524	76,570,476
1911	82,342,000	4,182,150	78,159,850
1912	96,679,000	4,944,164	91,734,836
1913	101,647,000	5,234,820	96,412,180
1914	99,397,000	5,154,728	94,242,272
1915	103,237,000	5,390,004	97,847,000
1916	108,383,000	5,697,694	102,685,310
1917	99,672,000	5,275,639	94,396,361
1918	107,902,000	5,749,019	102,152,980
1919	116,117,000	6,228,516	109,888,480
1920	113,066,000	6,105,564	106,960,440
1921	137,734,000	7,487,220	130,246,780
1922	157,322,000	8,607,087	148,714,130
1923	178,073,000	9,806,480	168,266,520
1924	202,612,511	11,228,785	191,383,720
1925	208,895,772	11,652,206	197,243,566
1926	209,731,445	11,774,323	197,957,122
1927	220,309,868	12,447,504	207,862,364

* When available, these amounts have been taken from annual reports of the Minnesota State Department of Agriculture, Dairy and Food. If not available at the time required, receipts were estimated by the methods outlined in the text.

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[21] Business Practices and Management Problems of Creameries (mimeographed), J. D. Black, Paul L. Miller, B. A. Holt, University of Minnesota, pp. 60-62. In a study of the distribution of 20 million pounds of butter produced by 87 Minnesota creameries in 1919 and 1920, an average of 5.4 per cent was sold to patrons.

assumption that the amounts approximately balance probably leads to no appreciable error.

The amounts of butterfat received by Minnesota creameries, the amount deducted for resales to farmers, and the amounts representing the sales of the farmers of Minnesota are shown in Table 62.

The monthly production of creamery butter in Minnesota from 1921-1925 has been used as a basis for the percentage distributions of annual sales for this period. For 1926 and subsequent years, the percentage distributions have been based on the number of pounds of butter inspected monthly by the Land O'Lakes Creameries, Incorporated. These percentages are shown in Table 63, together with an average for 1921 to 1926, which was applied in the period prior to 1921.

The monthly sales of butterfat, as thus estimated, are shown in Table 64.

Table 63

Monthly Percentage Marketings of Butter Based on Production of Creamery Butter in Minnesota, 1921-1926

Month	1921	1922	1923	1924	1925	1926	Average
January	5.3	6.9	8.6	6.6	7.0	8.3	7.1
February	5.6	6.7	6.5	7.3	6.8	8.7	6.9
March	6.6	7.9	8.1	8.0	7.8	10.5	8.2
April	7.3	7.3	7.8	8.1	8.3	9.9	8.1
May	10.9	11.4	10.1	9.5	10.5	10.9	10.6
June	13.8	13.4	12.3	11.4	12.4	11.6	12.5
July	11.3	12.1	10.9	11.7	11.8	9.7	11.2
August	10.8	9.1	9.4	10.9	9.2	7.6	9.5
September	8.3	7.4	7.4	7.9	7.1	6.0	7.4
October	7.3	6.2	6.6	6.7	6.5	5.1	6.4
November	6.1	5.4	5.8	5.3	5.8	5.0	5.6
December	6.7	6.0	6.5	6.6	6.8	6.7	6.5

Table 64

Amount of Butterfat Sold Monthly by the Farmers of Minnesota,* 1910-1927 (Pounds)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	5,436,504	5,549,349	6,513,173	6,845,265	6,691,201	6,947,137	7,290,657	6,702,142	7,252,862
February	5,283,363	5,393,030	6,329,704	6,652,440	6,502,717	6,751,443	7,085,286	6,513,349	7,048,556
March	6,278,779	6,409,108	7,522,257	7,905,799	7,727,866	8,023,454	8,420,195	7,740,502	8,376,544
April	6,202,209	6,330,948	7,430,522	7,809,387	7,633,624	7,925,607	8,317,510	7,646,105	8,274,391
May	8,116,470	8,284,944	9,723,893	10,219,691	9,989,681	10,371,782	10,884,643	10,006,014	10,828,216
June	9,571,310	9,769,981	11,466,854	12,051,522	11,780,284	12,230,875	12,835,664	11,799,545	12,769,122
July	8,575,893	8,753,903	10,274,302	10,798,164	10,555,134	10,958,864	11,500,755	10,572,392	11,441,134
August	7,274,195	7,425,186	8,714,809	9,159,157	8,953,016	9,295,465	9,755,104	8,967,654	9,704,533
September	5,666,215	5,783,829	6,788,378	7,134,501	6,973,928	7,240,678	7,598,713	6,985,331	7,559,321
October	4,900,510	5,002,230	5,871,030	6,170,380	6,031,505	6,262,208	6,571,860	6,041,367	6,537,791
November	4,287,947	4,376,952	5,137,151	5,399,082	5,277,567	5,479,432	5,750,377	5,286,196	5,720,567
December	4,977,081	5,080,390	5,962,764	6,266,792	6,125,748	6,360,055	6,674,545	6,135,763	6,639,944
Total	76,570,476	78,159,850	91,734,837	96,412,180	94,242,271	97,847,000	102,685,309	94,396,360	102,152,981

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	7,802,082	7,594,191	6,903,079	10,261,275	14,470,921	12,631,326	13,807,050	16,430,441	16,836,852
February	7,582,305	7,380,270	7,293,820	9,963,847	10,937,324	13,971,012	13,412,562	17,222,269	16,213,264
March	9,010,855	8,770,756	8,596,287	11,748,416	13,629,588	15,310,698	15,384,998	20,785,498	17,876,163
April	8,900,967	8,663,796	9,508,015	10,856,131	13,124,789	15,502,081	16,371,216	19,597,755	18,915,475
May	11,648,179	11,337,807	14,196,899	16,953,411	16,994,919	18,181,453	20,710,574	21,577,326	23,488,447
June	13,736,060	13,370,055	17,974,056	19,927,693	20,696,782	21,817,744	24,458,202	22,963,026	25,567,070
July	12,307,510	11,979,569	14,717,886	17,994,410	18,341,051	22,391,895	23,274,741	19,201,841	22,449,135
August	10,439,406	10,161,242	14,066,652	13,532,986	15,817,053	20,860,825	18,146,408	15,044,741	17,668,302
September	8,131,748	7,915,073	10,810,483	11,004,846	12,451,722	15,119,314	14,004,293	11,877,427	12,679,604
October	7,032,863	6,845,468	9,508,015	9,220,276	11,105,590	12,822,709	12,820,832	10,095,813	12,471,742
November	6,153,755	5,989,785	7,945,054	8,030,563	9,759,458	10,143,337	11,440,127	9,897,856	10,393,118
December	7,142,751	6,952,429	8,726,534	8,922,848	10,937,324	12,631,326	13,412,562	13,263,127	13,303,192
Total	109,888,481	106,960,441	130,246,780	148,416,702	168,266,521	191,383,720	197,243,565	197,957,120	207,862,364

* Calendar year totals which result from the addition of the 12 months frequently do not agree exactly with the yearly totals originally given, owing to slight deviations above or below 100 of the total percentage distribution for an individual year.

Since September, 1920, the prices used for butterfat are those of the 15th of the month reported by the United States Department of Agriculture. Previous to September, 1920, the monthly price of butterfat in Minnesota was assumed to be equal to the average price of 92 score butter in New York. This relationship was found to be approximately correct for the period 1920 to 1926, when prices of both Minnesota butterfat and 92 score butter in New York were available for comparison. Table 65 shows the price used for butterfat in Minnesota, which is a combination of the two series mentioned.

Table 65

Estimated Prices for Butterfat Received by Producers in Minnesota,* 1910-1927

(Per pound)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	$0.33	$0.26	$0.39	$0.35	$0.33	$0.34	$0.33	$0.40	$0.52
February	.30	.26	.32	.36	.29	.32	.34	.44	.50
March	.33	.24	.31	.37	.28	.30	.37	.42	.44
April	.31	.21	.33	.35	.25	.31	.36	.44	.42
May	.28	.22	.30	.29	.26	.29	.31	.40	.42
June	.28	.23	.27	.28	.27	.28	.30	.39	.44
July	.28	.25	.27	.27	.28	.27	.29	.39	.45
August	.29	.26	.27	.28	.30	.26	.31	.41	.46
September	.30	.27	.30	.32	.31	.27	.34	.44	.56
October	.30	.30	.31	.31	.32	.29	.35	.45	.58
November	.31	.34	.34	.34	.35	.31	.39	.46	.63
December	0.30	0.37	0.37	0.36	0.34	0.35	0.40	0.50	0.69

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	$0.62	$0.65	$0.47	$0.38	$0.50	$0.54	$0.41	$0.47	$0.52
February	.52	.66	.43	.37	.46	.53	.37	.45	.51
March	.62	.67	.43	.36	.47	.49	.43	.45	.51
April	.64	.71	.42	.34	.47	.41	.42	.43	.51
May	.58	.61	.29	.34	.41	.38	.41	.41	.48
June	.52	.57	.28	.34	.38	.37	.42	.42	.44
July	.53	.57	.33	.35	.37	.39	.42	.41	.44
August	.55	.55	.39	.34	.40	.39	.43	.41	.43
September	.59	.57	.39	.35	.43	.38	.44	.43	.45
October	.68	.60	.40	.38	.46	.37	.49	.46	.48
November	.71	.57	.42	.44	.50	.38	.49	.48	.49
December	0.72	0.56	0.41	0.50	0.53	0.43	0.52	0.52	0.52

* January, 1910, to August, 1920, price of New York Extras, 1926 Yearbook of Agriculture. September, 1920, to December, 1925, price received by producers (fifteenth of the month), U. S. Dept. of Agr. Statistical Bull. 15; 1926-27, current numbers of Crops and Markets.

Milk

The amount of fluid milk sold by the farmers of Minnesota was estimated by combining the sales within the Twin City area, the sales in Minnesota cities outside the Twin City area, and the sales to cheese factories. The basic data were such that the separate computation of milk in each of these divisions was feasible. Estimates of urban consumption of milk furnish the basis for the amount of milk sold by Minnesota farmers. Urban consumption for the Twin Cities was determined by reducing the population to adult male equivalents, by a method similar to that previously explained, and applying a consumption figure. Several sources were consulted in the effort to determine consumption per equivalent adult male in the Twin Cities. The basis for the estimate finally adopted was the per capita consumption of milk in Minneapolis for the years 1912 and 1923.[22] These per capita estimates of consumption were reduced to the basis of consumption per equivalent adult male, and straight line interpolation used for the intervening years. The same annual increment of change was used to extend the figures back to 1910 and forward to 1926. As thus estimated, the consumption of milk per equivalent adult male in the Twin Cities ranged from 325 pounds in 1910 to 349 pounds in 1926.

After the total milk consumed in the Twin City area was estimated in this manner, the amount of milk sold to distributors[23] by the Twin City Milk Producers' Association was subtracted. The difference represented the amount of milk sold in the Twin Cities that was received from sources other than the association. To this difference was added the total milk received by the association. This would include not only the milk that organization sold to distributors within the cities but also milk sold in the area that was disposed of in other ways. This sum, which could be computed for the years 1918 to 1927, represents the total milk sold by farmers in the Twin City area. Before 1918, the first full year of operation of the Twin City Milk Producers' Association, the milk sold in the Twin City area was assumed to equal the total consumption of milk in the Twin Cities, estimated on the basis of population and the consumption per equivalent adult male. The estimate based on this assumption fails to include any surplus taken care of by individual dealers.

Sales of milk for the area outside the Twin Cities were estimated as follows: The total annual population of cities and towns of more than 2,500 population in 1920 was determined for each year by means of interpolation between census years. The annual population was reduced to adult male equivalents and the consumption of milk was derived by applying an annual consumption of 340 pounds per adult male to the total adult male equivalents for each year. Sales were assumed to be equal to consumption.

The annual amount of milk purchased by cheese factories within the state is reported by the State Dairy and Food department, or can be computed approximately by the amount of cheese manufactured.

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[22] C. M. Jones, The Milk Supply of Minneapolis, Bull. 53, State Dairy and Food Commission, p. 5; and 1925 Yearbook, Franklin Co-operative Creamery Association, p. 33.

[23] Twin City Milk Producers' bulletins.

The sum of these three estimates represents the total amount of milk sold annually by the farmers of Minnesota. These amounts are shown later as the totals in Table 67, where they have been distributed according to months.

The reports of the total amounts of milk handled by the Twin City Milk Producers' Association were available by months in their original form. In the case of annual figures, or estimates of consumption which had to be made on an annual basis, it was necessary to apply a monthly percentage distribution before the various figures could be combined to form the total sales of milk. The amount of milk sold in the Twin Cities which was secured from other sources than the Twin City Milk Producers' Association was distributed according to the percentage which the sales to distributors by the association for each month were of the total annual sales. The milk used in cities other than Minneapolis and St. Paul was distributed according to the average of the above percentages for the period 1918-1926. In the case of milk sold for the manufacture of cheese, it was thought advisable to make the monthly distribution on the basis of the average percentage which the amount of milk received each month by the Twin City Milk Producers' Association was of the total annual amount, rather than on the basis of their sales to distributors. The average percentage distributions of the two series are shown in Table 66.

Table 66

Average Monthly Percentage Marketings of Milk, 1918-1926

	Based on T.C.M.P.A. sales to distributors	Based on total amount handled by T.C.M.P.A.
January	7.7	7.9
February	7.2	7.8
March	8.0	8.9
April	8.1	8.5
May	8.6	10.0
June	8.6	10.3
July	9.1	9.1
August	8.7	7.9
September	8.5	7.1
October	8.7	7.2
November	8.5	7.1
December	8.3	8.2

Table 67

Amount of Milk Sold Monthly by the Farmers of Minnesota, 1910-1927 (Hundredweight)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	223,615	220,479	230,470	243,721	252,720	256,274	261,080	267,919	292,218
February	211,117	207,778	217,427	230,255	238,940	242,212	246,717	253,248	277,573
March	235,702	231,778	242,671	257,173	266,976	270,582	275,593	282,928	309,449
April	236,155	232,675	243,325	257,465	267,057	270,772	275,832	283,089	296,208
May	255,488	250,854	262,884	278,933	289,754	293,575	298,976	307,003	343,037
June	256,951	252,028	264,280	280,647	291,666	295,448	300,857	308,983	347,147
July	263,120	259,641	271,274	286,683	297,163	301,394	307,067	315,071	350,288
August	247,653	245,097	255,627	269,510	279,005	283,151	288,551	295,941	322,825
September	238,945	237,043	246,872	259,779	268,651	272,781	278,040	285,054	299,490
October	244,240	242,357	252,370	265,509	274,546	278,780	284,161	291,319	293,085
November	238,945	237,043	246,872	259,779	268,651	272,781	278,040	285,054	284,142
December	239,501	236,424	246,960	260,908	270.403	274,274	279,445	286,712	286,166
Total	2,891,432	2,853,197	2,981,032	3,150,362	3,265,532	3,312,024	3,374,359	3,462,321	3,701,628

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	318,130	305,445	314,422	334,574	366,751	429,311	439,989	495,024	470,013
February	308,629	297,655	310,489	317,605	349,992	420,746	416,893	473,172	450,201
March	352,943	332,052	360,525	360,404	401,239	463,266	471,380	529,482	507,065
April	339,320	326,392	368,290	345,941	397,073	456,060	468,452	510,783	489,847
May	390,405	364,346	420,913	392,558	443,826	500,983	528,979	562,315	552,229
June	394,642	379,527	430,237	389,502	453,523	506,217	540,409	549,695	553,351
July	391,637	365,850	397,732	362,615	428,056	471,581	510,090	506,174	509,690
August	364,628	336,091	366,216	336,545	399,201	418,783	445,033	453,968	440,176
September	333,331	324,521	340,346	321,097	371,893	397,191	402,155	415,455	416,344
October	341,593	330,659	347,236	337,179	381,146	408,142	417,138	424,190	426,615
November	340,817	319,480	336,060	326,669	384,527	396,902	421,905	419,973	417,732
December	365,229	331,233	364,414	348,246	419,272	427,967	463,630	459,852	451,630
Total	4,241,304	4,013,251	4,356,880	4,172,935	4,796.499	5,297,149	5,526,053	5,800,083	5,684,893

The monthly average prices of milk are the weighted average prices paid producers for milk of each of the three divisions, weighted by the amounts of each sold by producers. From April, 1917, to December, 1927, the monthly price of milk in the Twin City area was assumed to be the price paid producers by the Twin City Milk Producers Association. The monthly price of milk outside the Twin City area from April, 1917, to December, 1927, was taken as the average price paid producers in the West North Central States reported in Crops and Markets and previous publications of the United States Department of Agriculture. Prior to these periods the price of milk for both areas was computed according to a formula relating the price of butter to the price of milk.

Table 68

Monthly Weighted Price of Milk Received by Producers in Minnesota,* 1910-1927

(Fifteenth of the month)

(Per hundredweight)

Month	1910	1911	1912	1913	1914	1915	1916	1917	1918
January	$1.57	$1.30	$1.83	$1.65	$1.60	$1.66	$1.70	$2.30	$2.73
February	1.46	1.30	1.57	1.68	1.46	1.58	1.73	2.42	2.64
March	1.56	1.23	1.54	1.71	1.43	1.51	1.82	2.35	2.46
April	1.47	1.10	1.59	1.61	1.29	1.51	1.76	2.24	2.33
May	1.35	1.12	1.46	1.39	1.30	1.43	1.57	2.03	2.25
June	1.36	1.17	1.36	1.37	1.35	1.41	1.57	1.95	2.28
July	1.38	1.25	1.38	1.35	1.41	1.39	1.54	2.17	2.35
August	1.42	1.30	1.39	1.40	1.49	1.37	1.62	2.30	2.50
September	1.47	1.34	1.51	1.55	1.53	1.42	1.75	2.36	2.77
October	1.48	1.46	1.55	1.52	1.58	1.50	1.79	2.70	3.03
November	1.51	1.61	1.66	1.63	1.68	1.57	1.93	2.58	3.24
December	1.47	1.70	1.76	1.69	1.64	1.70	1.95	2.65	3.39

Month	1919	1920	1921	1922	1923	1924	1925	1926	1927
January	$3.20	$3.08	$2.50	$1.90	$2.51	$2.34	$2.13	$2.25	$2.33
February	2.72	2.96	2.38	1.82	2.37	2.27	2.12	2.17	2.32
March	2.99	2.80	2.28	1.81	2.35	2.12	2.14	2.13	2.32
April	2.85	2.81	2.16	1.78	2.25	1.81	2.10	2.03	2.32
May	2.73	2.65	1.76	1.73	2.17	1.76	2.06	2.01	2.15
June	2.85	2.60	1.55	1.70	2.15	1.80	2.08	2.04	2.09
July	2.93	2.61	1.72	1.85	2.19	1.83	2.09	2.11	2.13
August	3.05	3.04	1.98	1.95	2.50	2.04	2.20	2.15	2.18
September	3.13	3.12	2.07	2.16	2.48	2.05	2.37	2.21	2.25
October	3.09	3.12	2.03	2.30	2.45	2.05	2.45	2.27	2.37
November	3.16	3.07	2.01	2.38	2.39	2.06	2.47	2.33	2.39
December	3.21	2.94	1.94	2.55	2.34	2.13	2.46	2.36	2.42

* Prices include those of Twin City Milk Producers' Association, those reported by Crops and Markets for the west north central section, those of the State Department of Agriculture, Dairy and Food, and others, weighted by amounts of milk sold, as explained in text.

The annual average price paid producers for milk sold to cheese factories is reported by the State Department of Agriculture, Dairy and Food. It was assumed that the monthly price of milk sold to cheese factories varied from the annual average in the same proportion that the price of cheese at New York varied from the average annual price of cheese. Prices of cheese used as a basis for determining these monthly variations in the milk price were obtained from the New York Produce Review. The weighted price of all milk, derived as explained above, is shown in Table 68.

The data of prices and quantities of milk sold as herein estimated are undoubtedly subject to considerable error. However, no more satisfactory method of their determination has been found. Actual reports of sales are not available. Census data of milk sales are doubtless too low, according to statements of the bureau itself. Hence, it was found necessary to devise methods of estimation based upon sources other than the census.

There is some duplication of reported sales, because part of the milk received by the Twin City Milk Producers' Association eventually finds its way into butter or cheese production and is reported there, also. On the other hand, no attempt is made to estimate the amount of milk sold in towns of under 2,500 population. Neither has any attempt been made to include amounts of farm butter, buttermilk, homemade cheese, and other dairy products sold by farmers. These items are small and are continually becoming of less importance. The duplications and omissions in dairy products tend to offset one another. It is probable that omissions more than offset duplications. It was also assumed that the amount of milk and cream shipped into the state would balance that which is shipped out of the state by farmers. No data are available to prove this assumption, but estimates of dairy specialists indicate that the two about offset each other.

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